ENVIRONMENTAL AND GEOLOGICAL CONTROLS ON THE DIVERSITY AND DISTRIBUTION OF THE SAUROPODOMORPHA

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I, Philip David Mannion, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

Sauropodomorph dinosaurs were an important component of Mesozoic terrestrial ecosystems. Their diversity and abundance fluctuated throughout the Mesozoic but whether this reflects genuine biological changes or merely variations in our sampling of the rock record is uncertain. A database of all sauropodomorph individuals (2335) has been compiled, including environmental, geological, taxonomic and taphonomic data. Using a variety of sampling proxies (including a new specimen completeness metric) and a number of analytical techniques (residuals, rarefaction and phylogenetic diversity estimates), this work has demonstrated that sauropodomorph diversity appears to be genuinely high in the Pliensbachian-Callovian and Kimmeridgian-Tithonian, while low diversity levels are recorded for the Oxfordian and Berriasian-Barremian, with the J/K boundary seemingly representing a real diversity crash. Diversity in the remaining Triassic-Jurassic stages appears to be largely controlled by sampling biases while Late Cretaceous diversity is difficult to elucidate and perhaps remains relatively under-sampled. Sea level affects diversity and abundance in the Jurassic-Early Cretaceous, but does not appear to be linked in the Late Cretaceous. Different clades of sauropodomorphs potentially preferred different environments and this may have had an effect on changes in their distribution and diversity. Titanosaurs have been demonstrated to show a preference for inland environments compared to non-titanosaurs, and it is possible that this led to their success in the Cretaceous when other sauropod clades were in decline. An assessment of the palaeolatitudinal patterns of sauropods and ornithischians reveals a distributional skew in the Late Cretaceous, which may reflect environmental and/or dietary preferences. A study of completeness through historical time contradicts the recent claim that the quality of dinosaurian type material has improved from the 19th century to the present. These studies illustrate that use of a number of techniques is imperative in any attempt to tease apart genuine patterns from the biases of an uneven rock record.

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CHAPTER ONE

INTRODUCTION AND REVIEWS

Introduction to the Sauropodomorpha

Sauropodomorpha is a major clade of non-avian Mesozoic dinosaurs composed of gigantic, herbivorous, terrestrial forms (though see later discussion on feeding) (Fig. 1.1). Sauropodomorpha is the sister group of Theropoda, which together comprise the Saurischia. This latter clade split from the other clade of dinosaurians (the Ornithischia) probably sometime in the Ladinian (Middle Triassic) (Martinez and Alcober 2009). Sauropodomorpha is diagnosed by the following synapomorphies: (1) skull length less than 50% of femur length, (2) possession of a flat caudoventrally-facing area on the coracoid between the glenoid and the coracoid tubercle, and (3) pubic peduncle of the ilium is at least twice as long as its craniocaudal width (Upchurch *et al*. 2007a). It includes the largest terrestrial animals of all time (Wilson 2002; Upchurch *et al*. 2004a), with *Argentinosaurus* (body mass of >70 tonnes; Mazzetta *et al*. [2004]) a notable example. Their remains have been found on all continents and by the Middle Jurassic (and probably by the Early Jurassic: only Australia currently lacks Early Jurassic sauropodomorph remains) they had achieved a global distribution (Upchurch 1995; Upchurch *et al*. 2002, 2004a; Weishampel *et al*. 2004a).

The earliest known sauropodomorphs are *Saturnalia* and *Panphagia* from the early Carnian (Late Triassic) of Brazil and Argentina, respectively (Langer *et al*. 1999; Martinez and Alcober 2009). An earlier record from the Middle Triassic of Madagascar (Flynn *et al*. 1999) has since been shown to represent a non-dinosaurian archosauromorph (Flynn *et al*. 2008). An early diversity peak comprised of basal sauropodomorphs and 'prosauropods' (e.g. *Thecodontosaurus*, *Mussaurus* and *Plateosaurus*) in the Norian (Late Triassic) was followed by a drop in the Rhaetian, before a prominent Early Jurassic increase (Weishampel and Jianu 2000; Barrett and Upchurch 2005; Barrett *et al*. 2009). Non-eusauropod sauropodomorphs (including 'prosauropods'; Fig. 1.1) became extinct prior to the Middle Jurassic (with the possible exception of "*Yunnanosaurus*" *youngi*; Lü *et al*. 2007a), coincident with the onset of a eusauropod radiation (Sereno 1999; Barrett

and Upchurch 2005). Note that these taxa became extinct regardless of whether they are considered monophyletic or a paraphyletic assemblage (see below); only the nature of this extinction may in some respects be a taxonomic artefact (see Forey *et al*. 2004).

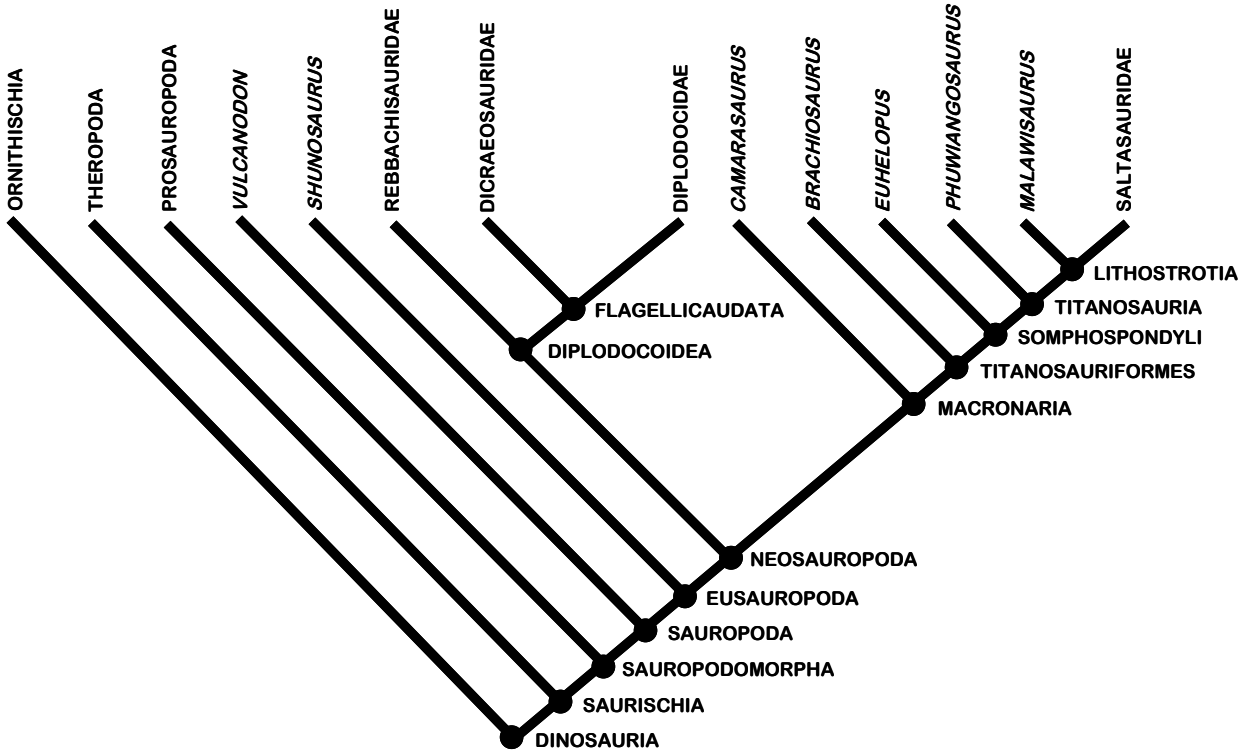

FIGURE 1.1. Simplified cladogram showing the relationships between the major sauropodomorph lineages and the stem- and node-based names currently in use (based on Wilson and Upchurch 2003, 2009; Upchurch *et al*. 2004a, 2007a).

Several studies have noted a Middle Jurassic peak in sauropod diversity (Hunt *et al*. 1994; Barrett and Willis 2001; Upchurch and Barrett 2005), which may reflect a neosauropod radiation (Figs. 1.1 and 1.2). The Oxfordian (early Late Jurassic) represents an apparent diversity trough (Upchurch and Barrett 2005; Barrett *et al*. 2009), while the remaining Late Jurassic stages (Kimmeridgian-Tithonian) are typically thought to have represented the highest peak in diversity (Fig. 1.2) (Bakker 1977, 1978; Horner 1983; Weishampel and Horner 1987; Haubold 1990; Hunt *et al*. 1994; Upchurch 1995; Sereno

1997, 1999; Wilson and Sereno 1998; Weishampel and Jianu 2000; Barrett and Willis 2001; Upchurch and Barrett 2005; Barrett *et al*. 2009), exemplified by well known taxa such as *Brachiosaurus* and *Diplodocus*.

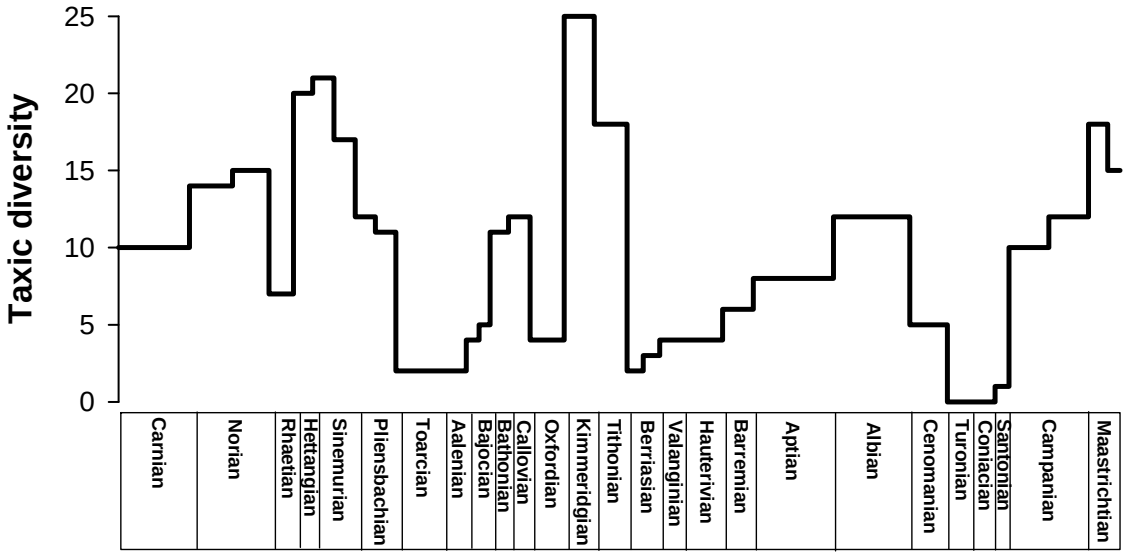

FIGURE 1.2. Sauropodomorph taxic diversity through the Mesozoic based on taxa included in Barrett and Upchurch (2005) and Upchurch and Barrett (2005).

A prominent decline in the number of genera across the Jurassic/Cretaceous (J/K) boundary is dictated by the apparently reduced species richness of the earliest Cretaceous (Fig. 1.2: Hunt *et al*. 1994; Wilson and Sereno 1998; Upchurch and Barrett 2005; Barrett *et al*. 2009). Sauropods underwent a major diversification in the mid-Cretaceous (Fig. 1.2), with this radiation predominantly composed of titanosaurs (Salgado *et al*. 1997; Wilson and Upchurch 2003; Curry Rogers 2005; Upchurch and Barrett 2005; Lloyd *et al*. 2008), as well as a small contribution from rebbachisaurid diplodocoids (Upchurch and Barrett 2005; Sereno *et al*. 2007; Mannion 2009a) (Fig. 1.1). Diversity apparently dropped in the mid-Late Cretaceous before reaching another peak in the Campanian–Maastrichtian (Hunt *et al*. 1994; Weishampel and Jianu 2000; Barrett and Willis 2001; Upchurch and Barrett 2005), although this peak is smaller than that in

the Late Jurassic. There is also evidence for a decline in sauropod diversity prior to their final extinction at the Cretaceous/Paleogene (K/P) boundary (Fig. 1.2: Upchurch and Barrett 2005; Barrett *et al*. 2009).

Monophyly of Sauropodomorpha

The name Sauropodomorpha was coined by Huene (1932) for a group composed of sauropods and some 'prosauropods'. The first cladistic study of dinosaurs supported this monophyletic grouping (Gauthier 1986), a conclusion confirmed by later computer-based analyses (Sereno 1999; Langer 2004). Although agreement has been reached on the monophyly of sauropodomorphs, there has been little consensus as to the interrelationships between sauropods and prosauropods. Two possibilities have been proposed: either prosauropods are a monophyletic clade that is the sister group of Sauropoda or they are a paraphyletic grade consisting of successively distant outgroups to sauropods (Gauthier 1986; Galton 1990; Gauffre 1993; Sereno 1999; Benton *et al*. 2000; Yates 2003a, 2004, 2007; Yates and Kitching 2003; Galton and Upchurch 2004; Langer 2004; Upchurch *et al*. 2007a). Upchurch *et al*. (2007a) found evidence for a basal grade of sauropodomorphs (comprised of *Saturnalia*, *Thecodontosaurus*, *Mussaurus* and *Efraasia*), with the remaining taxa divided into two monophyletic sister groups (a 'prosauropod' and sauropod clade) (Fig. 1.3). Other analyses (Yates 2003a, 2004, 2007; Yates and Kitching 2003) found a similar grade of basal sauropodomorphs, but recovered tree topologies where 'prosauropods' formed a completely paraphyletic array with respect to sauropods (Fig. 1.4; see 'Taxonomic Revision'). These recent analyses have also demonstrated that several taxa previously considered 'traditional' prosauropods are in fact basal sauropodomorphs (e.g. *Thecodontosaurus*, *Mussaurus* and *Efraasia*) and others early sauropods (e.g. *Blikanasaurus*, *Melanorosaurus*, *Camelotia* and *Lessemsaurus*).

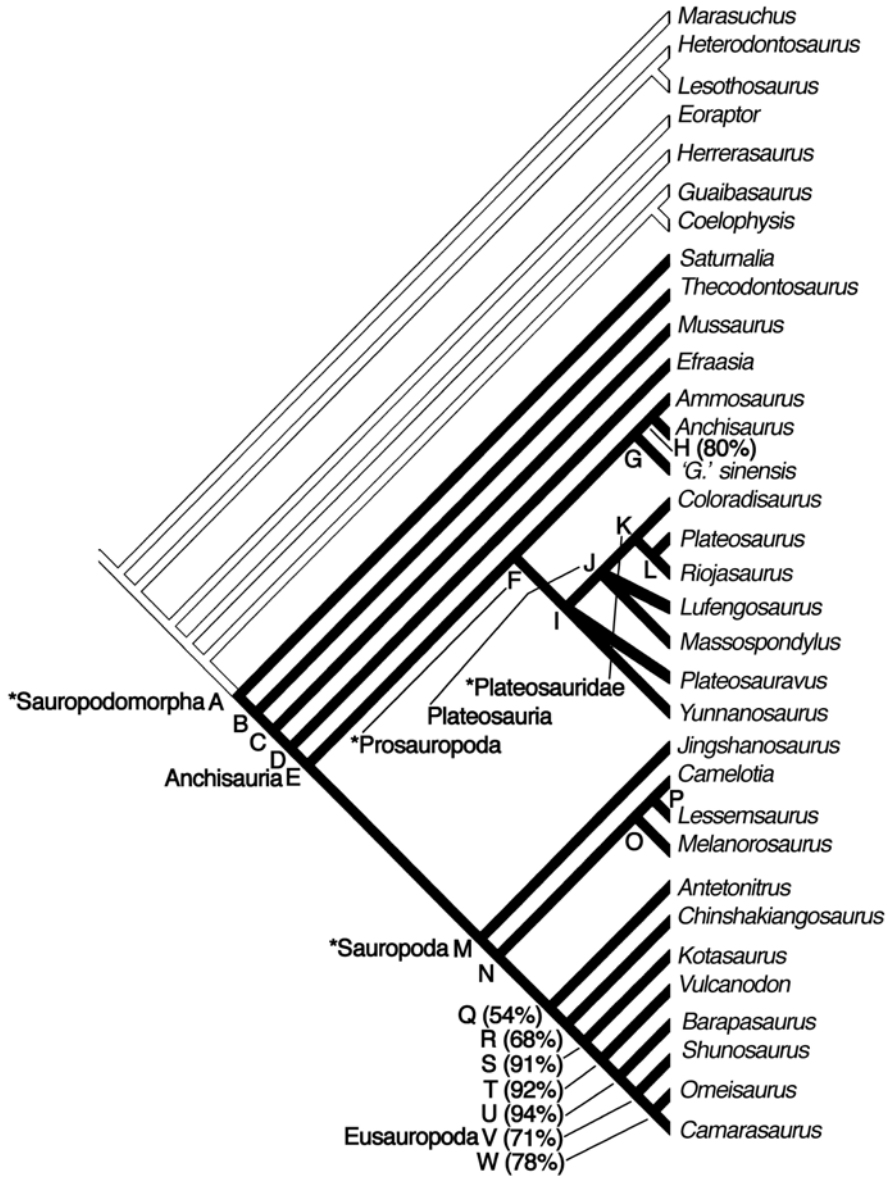

FIGURE 1.3. Strict consensus cladogram depicting the phylogenetic relationships of basal sauropodomorphs found by Upchurch *et al*. (2007a). See Upchurch *et al*. (2007a) for particular details pertaining to the cladogram.

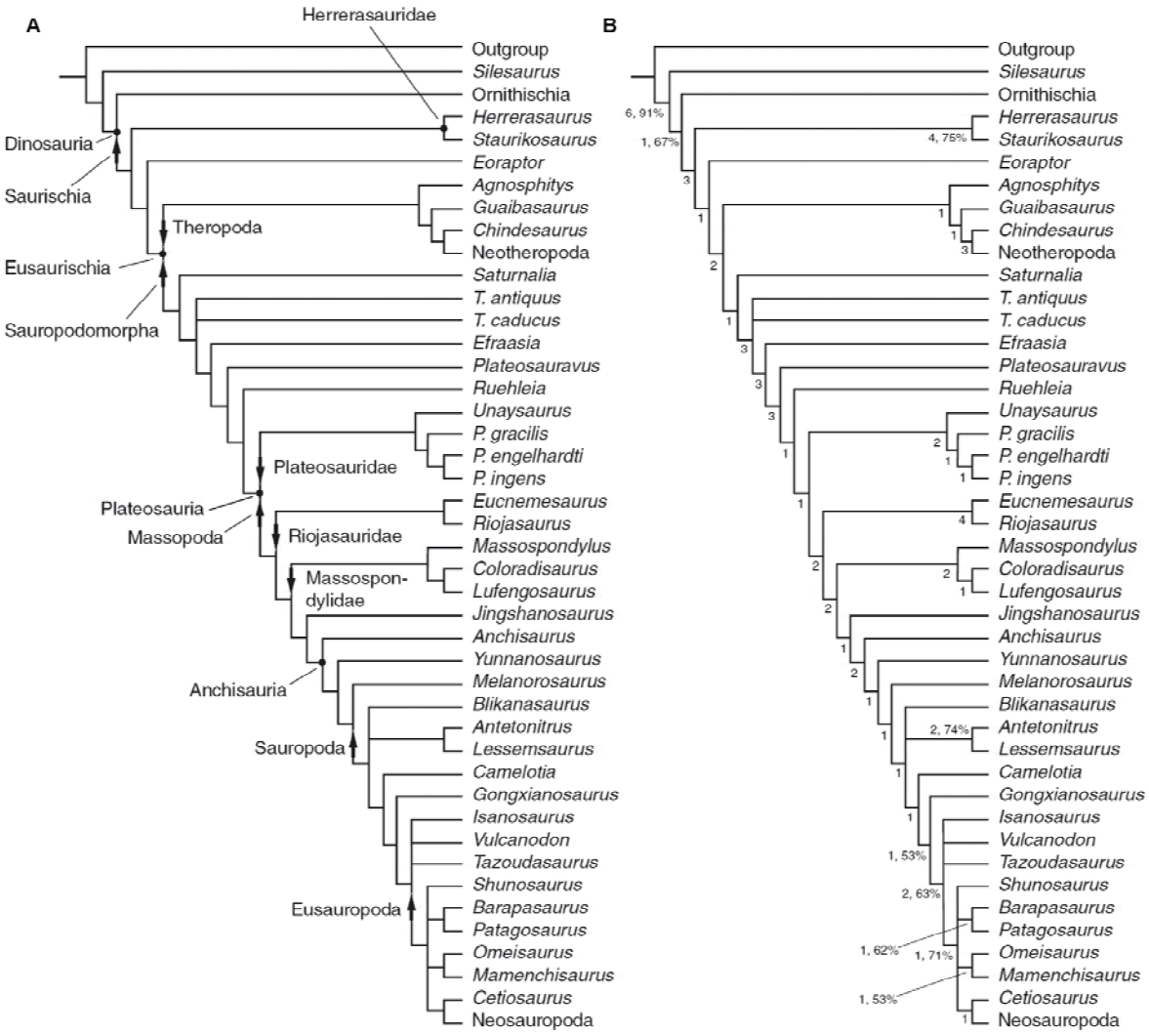

FIGURE 1.4. Strict consensus cladogram depicting the phylogenetic relationships of basal sauropodomorphs found by Yates (2007): (A) cladogram applied with phylogenetic taxonomy; (B) cladogram with robustness measures. See Yates (2007) for particular details pertaining to the cladogram.

Feeding, stance and size

Basal sauropodomorphs, 'prosauropods' and basal sauropods were probably bipedal or facultatively bipedal (e.g. *Efraasia*, *Thecodontosaurus*, *Jingshanosaurus* and *Melanorosaurus*). However, many of these are quite small-bodied animals; larger

sauropodomorphs (e.g. the prosauropod *Riojasaurus*) were probably fully quadrupedal (Barrett and Upchurch 2007). Sauropods more derived than basal sauropods were almost certainly all quadrupedal. Basal sauropodomorphs are considered to have been facultative herbivores or omnivores (Barrett 2000). Prosauropods and basal sauropods retain the same feeding structures as basal sauropodomorphs but tend to have an increased body size, suggesting a greater dependence on an herbivorous diet; however, it has been suggested that omnivory may still have been important in some of these taxa (Barrett 2000; Barrett and Upchurch 2007). More derived sauropodomorphs demonstrate evidence for obligate herbivory. This overall switch to obligate quadrupedalism and herbivory correlates with an increase in sauropodomorph size (*Thecodontosaurus* and *Riojasaurus* were approximately 1.5-2m and 8m in length, respectively; Barrett and Upchurch 2007), which in turn probably reflects a shift towards bulk processing of large quantities of vegetation and the need for a larger trunk region for digestion (Galton and Upchurch 2004; Barrett and Upchurch 2007; Upchurch *et al*. 2007a, b). However, it is worth noting that recent work has suggested that *Saturnalia* (which is approximately 1.5m in length and considered the most basal sauropodomorph known; Langer *et al*. 1999; Galton and Upchurch 2004) may have been quadrupedal (Barrett and Upchurch 2007). Hatchlings of the 'prosauropod' *Massospondylus* were almost certainly obligate quadrupeds (Reisz *et al*. 2005) and this may also have been the case for hatchlings of the basal sauropodomorph *Mussaurus* (Barrett and Upchurch 2007; note that adult specimens of this taxon are not known).

The general morphology of sauropodomorphs remained relatively consistent throughout their evolutionary history. This *bauplan* consisted of a long neck and tail either end of a large barrel-shaped body, with a relatively small skull in proportion to the size of the animal (Wilson 2002; Galton and Upchurch 2004; Upchurch *et al*. 2004a). Only in basal sauropods (i.e. *Antetonitrus* and more derived sauropods) did the support of four columnar limbs develop (Barrett and Upchurch 2007), relating to increases in relative forelimb length. The neck elongation (by incorporation of additional cervicals

and/or the elongation of individual cervicals) that is so characteristic of sauropods became marked in eusauropods (Upchurch 1994; Wilson and Sereno 1998) and it is noteworthy that extreme neck elongation occurred in three separate sauropod radiations: diplodocids, *Omeisaurus* + *Mamenchisaurus* and a clade including *Euhelopus* + *Erketu* (Wilson and Upchurch 2009). This elongation is usually regarded as a key feeding adaptation (Upchurch and Barrett 2000), permitting enlarged feeding envelopes. Conversely, there is evidence that some sauropods reduced this elongation: *Brachytrachelopan* (a derived dicraeosaurid from the Late Jurassic of Patagonia; Rauhut *et al*. 2005) had a neck approximately 40% shorter than other known dicraeosaurids (though probably contained the same number of cervicals).

Sauropodomorph diversity

Basal sauropodomorphs and prosauropods

As discussed earlier, sauropodomorphs first peaked in diversity during the Late Triassic. This peak is primarily composed of basal sauropodomorphs and 'prosauropods'; the species richness of these animals subsequently declined in the Early Jurassic while sauropod diversity increased during this time period. These observations have led to the suggestion by some workers that sauropods out-competed basal sauropodomorphs and prosauropods, leading to the extinction of the latter by the end of the Early Jurassic (Barrett and Upchurch 2005); however, as noted above, if prosauropods are a paraphyletic assemblage, then this extinction may merely be a taxonomic artefact.

Eusauropods

The Middle Jurassic saw a large increase in sauropod diversity and this can largely be explained by the radiation of non-neosauropod eusauropods (including such forms as *Shunosaurus*, *Cetiosaurus*, *Omeisaurus* and *Chebsaurus*) (Barrett and Upchurch 2005).

Eusauropoda is a node-based taxon comprising the most recent common ancestor of *Shunosaurus* and *Saltasaurus* and all descendants of that ancestor (Upchurch 1995; Upchurch *et al*. 2004). Based on cranial evidence, these sauropods are inferred to have had a simple orthal jaw action that allowed powerful cropping of large amounts of vegetation (Calvo 1994; Barrett and Upchurch 1994, 1995, 2005; Upchurch and Barrett 2000). Non-neosauropod eusauropods were still present during the Late Jurassic and Early Cretaceous (e.g. *Mamenchisaurus* and *Hudiesaurus*), including the recently recognised eusauropod clade of turiasaurs which is considered to be comprised of *Turiasaurus*, *Galveosaurus* and *Losillasaurus* (Royo-Torres *et al*. 2006), though none are known from later than the Barremian.

Neosauropods

Neosauropods became the dominant sauropods in the Late Jurassic, although they originated at least as early as the Middle Jurassic based on a global array of body fossils and trackways (Santos *et al*. 1994; Day *et al*. 2002, 2004; Upchurch *et al*. 2004a; Weishampel *et al*. 2004a; Moser *et al*. 2006; see also Rauhut and López–Arbarello [2009] for a critical discussion). Neosauropoda is a node-based taxon defined as the most recent common ancestor of *Diplodocus* and *Saltasaurus* and all descendants of that ancestor (Bonaparte 1986; Wilson and Sereno 1998). They split into two radiations during the Middle Jurassic (Sereno 1999): the diplodocoids and macronarians (Upchurch 1998; Wilson and Sereno 1998).

Diplodocoids

Diplodocoids are comprised of diplodocids (e.g. *Apatosaurus*, *Barosaurus*, *Diplodocus* and *Australodocus*), dicraeosaurids (e.g. *Dicraeosaurus* and *Amargasaurus*) and rebbachisaurids (e.g. *Rebbachisaurus*, *Limaysaurus* and *Nigersaurus*). They are known from North and South America, Africa and Europe (Upchurch *et al*. 2004a; Weishampel

et al. 2004a), and recently evidence has been discovered for their presence in Asia (Upchurch and Mannion 2009). Diplodocoidea is a stem-based taxon defined as Neosauropoda more closely related to *Diplodocus* than to *Saltasaurus* (Wilson and Sereno 1998). Diplodocoids possess feeding mechanisms suited to the efficient raking of vegetation; their teeth are slender and cylindrical and their feeding apparatus show no evidence for extensive oral processing (Barrett and Upchurch 1994, 1995; Christiansen 2000; Upchurch and Barrett 2000). Diplodocoids were still present at least in the Coniacian (Late Cretaceous), represented by rebbachisaurids such as *Nopcsaspondylus* (Apesteguia 2007).

Macronarians and titanosauriforms

Basal macronarians include *Atlasaurus*, *Europasaurus* and possibly the Chinese sauropod *Bellusaurus* (Upchurch *et al*. 2004a; Sander *et al*. 2006), as well as the North American genus *Camarasaurus*. Macronaria is a stem-based clade defined as Neosauropoda more closely related to *Saltasaurus* than to *Diplodocus* (Wilson and Sereno 1998). The more derived macronarian clade consists of the titanosauriforms, basal forms of which include *Ornithopsis*, *Pelorosaurus* and *Huanghetitan* (Upchurch *et al*. 2004a; You *et al*. 2006). Titanosauriformes is a node-based taxon comprising the most recent common ancestor of *Brachiosaurus* and *Saltasaurus* and all descendants of that ancestor (Wilson and Sereno 1998). Basal titanosauriform teeth are intermediate between the narrow-crowned type of titanosaurs and diplodocoids and the broad-crowned type of most other sauropods, and were suited to cropping and 'nipping' vegetation (Barrett and Upchurch 2005). Titanosauriformes include two sauropod radiations: the brachiosaurids and the somphospondyls (Salgado *et al*. 1997; Wilson and Sereno 1998; Wilson 2002). Brachiosauridae includes the well known genus *Brachiosaurus*, as well as *Cedarosaurus*, *Sauroposeidon* and *Lusotitan*. Brachiosauridae is a stem-based taxon defined as Titanosauriformes more closely related to *Brachiosaurus* than to *Saltasaurus* (Wilson and Sereno 1998). Somphospondyli is comprised of titanosaurs as well as a clade of

more basal forms consisting of *Euhelopus*, *Erketu* and unnamed forms based on teeth from Spain and China (Wilson and Sereno 1998; Canudo *et al*. 2002; Barrett and Wang 2007; Wilson and Upchurch 2009).

Titanosaurs

Titanosauria is a node-based taxon defined as the most recent common ancestor of *Andesaurus* and *Saltasaurus* and all descendants of that ancestor (Wilson and Upchurch 2003). Titanosaurs are known from all continents except Antarctica. Although comprising approximately one-third of all sauropod genera, the interrelationships of titanosaurs are still poorly understood (Salgado *et al*. 1997; Upchurch 1998; Wilson and Sereno 1998; Sanz *et al*. 1999; Curry Rogers and Forster 2001; Wilson 2002, 2006; Wilson and Upchurch 2003; Upchurch *et al*. 2004a; Curry Rogers 2005; Calvo *et al*. 2007). Many of these phylogenies do seem to indicate that there is a general division between basal titanosaurs and more derived lithostrotians though, with taxa such as *Andesaurus* and *Phuwiangosaurus* included in the former category (Upchurch *et al*. 2004a; Curry Rogers 2005). Lithostrotia is a node-based taxon composed of the most recent common ancestor of *Malawisaurus* and *Saltasaurus* and all descendants of that ancestor (Upchurch *et al*. 2004a). It consists of taxa such as *Alamosaurus*, *Rapetosaurus*, nemegtosaurids (previously proposed by Upchurch [1999] as diplodocoids based on convergences in skull morphology, but now considered to be titanosaurs; Salgado and Calvo 1997; Wilson and Sereno 1998; Curry Rogers and Forster 2001; Wilson 2002, 2005; Curry Rogers 2005) and saltasaurids (Bonaparte and Powell 1980; Sereno 1998). The dentition of titanosaurs is superficially very similar to that of diplodocoids in that they both have very slender, peg-like teeth (Upchurch 1998), suited to the 'nipping' of vegetation (Barrett and Upchurch 2005). The earliest putative titanosaur skeletal remains are of the Kimmeridgian (Late Jurassic) Tendaguru (Tanzania) taxon *Janenschia*, which has been provisionally regarded as a basal titanosaur (Jacobs *et al*. 1993; Upchurch 1995; Wilson and Sereno 1998; Upchurch *et al*. 2004a). However, earlier

evidence of titanosaurs comes from the trackway record. The gait of titanosaurs has been demonstrated to be much wider than in non-titanosaurs (Wilson and Carrano 1999) and wide-gauge sauropod trackways (inferred as the products of titanosaurs; Wilson and Carrano 1999) have been described from the Middle Jurassic of Portugal and England (Santos *et al*. 1994; Day *et al*. 2002, 2004). However, it should be added that Henderson (2006) has argued that sauropods above a certain mass are responsible for these wide-gauge tracks, rather than just titanosaurs, and so it is possible that this earlier occurrence may be erroneous (see subsequent chapters for a more detailed discussion). Titanosaurs survived up until the K/P extinction event, with taxa such as *Magyarosaurus* found from the Late Maastrichtian of Romania.

Gregariousness

Evidence for a gregarious nature (Coombs 1990) comes from numerous bonebeds (e.g. the Morrison Formation of North America, the Kota Formation of India and the Lower Shaximiao Formation of China; Dodson *et al*. 1980a; Jain 1980; Xia *et al*. 1983; Xia and Li 1988) and vast trackway assemblages (Lockley *et al*. 1994 and references therein). Some of these bonebeds show evidence for different species living in close proximity to one another and a few tracksites demonstrate that some sauropods moved in multispecific herds (e.g. the Ardley tracksite in the UK shows both titanosaurs and non-titanosaurs moving in the same direction on the same bedding plane; Day *et al*. 2002, 2004). Differences in their palaeoecology, body size and feeding preferences probably enabled niche separation within these multispecific communities (Fiorillo 1991, 1998; Barrett and Upchurch 1995; Upchurch and Barrett 2000).

New research areas

Although a considerable amount of systematic, taxonomic and phylogenetic research has been carried out on sauropodomorphs (e.g. Wilson 2002; Upchurch *et al*. 2004a, 2007a; Curry Rogers 2005; Yates 2007), there has been limited work on the diversity of the group (e.g. Hunt *et al*. 1994; Upchurch and Barrett 2005; Barrett *et al*. 2009) and there is much scope for rigorous, quantitative analyses to be implemented. In addition, concern has been expressed that diversity merely mirrors fluctuations in the rock record (e.g. Raup 1972; Peters 2005; Smith and McGowan 2007) and, as such, it is important to compare sauropodomorph genus richness with a range of sampling proxies in an attempt to tease apart genuine diversity from the artefacts of a patchy rock record.

Different clades of sauropodomorphs may have potentially preferred different environments and this may have had an effect on changes in their distribution and diversity. Currently, only two studies have considered environmental preferences of sauropods. The first of these (Lockley *et al*. 1994) only examined the sauropod track record, while the only other analysis (Butler and Barrett 2008) was part of a larger study looking at Cretaceous herbivorous dinosaurs. Consequently, a study combining body fossil and tracksite data for sauropods across the entire Jurassic-Cretaceous would be novel and may allow insights into the different environments these animals lived in.

The Lockley *et al*. (1994) study (mentioned above) also analysed the distribution of sauropod tracksites and compared their abundance with fluctuations in sea level. In the subsequent years a large number of additional tracksites have been discovered, making an updated analysis timely and worthwhile, while body fossils have received little attention in previous distribution studies.

Lastly, no large-scale analyses of sauropodomorph taphonomy or disarticulation sequences have ever been implemented, with studies restricted to monospecific

bonebeds, geographical regions, or individual specimens (e.g. Sander 1992; Hungerbühler 1998; Heinrich 1999; González Riga and Astini 2007). However, there is potential for utilising the methods applied in experiments on modern-day carcasses (e.g. Hill 1979; Hill and Behrensmeyer 1984; Davis and Briggs 1998; Brand *et al*. 2003a) in an attempt to elucidate the taphonomic processes that large vertebrates such as sauropodomorphs underwent.

Review of previous environmental associations studies of sauropodomorphs

Introduction

Over the past two decades, our knowledge of sauropodomorph palaeoecology has been improved by the discovery of new material, the development of taxonomic schemes based on detailed phylogenetic analyses, and investigations of the depositional environments that yield sauropodomorph body fossils and trackways (see reviews in Galton and Upchurch 2004; Upchurch *et al*. 2004a; Carpenter and Tidwell 2005; Curry Rogers and Wilson 2005). Palaeoenvironmental analyses demonstrate that sauropodomorphs inhabited a wide variety of environments ranging from floodplain and fluvio-lacustrine settings in the Late Triassic Keuper successions of Germany (Sander 1992; Hungerbühler 1998) and Morrison Formation of North America (Dodson *et al*. 1980a, b), to near-shore estuarine conditions in the Tendaguru Formation of Tanzania (Russell *et al*. 1980). However, it is difficult to generalise about sauropodomorphs as a whole, or identify the habitat preferences of groups within Sauropodomorpha, because most studies have focused on a single geological formation (e.g. Dodson *et al*. 1980a, b) or geographical area (e.g. Lehman 1987; Lucas and Hunt 1989) (see also Butler and Barrett [2008] for a discussion of this issue). Consequently, one important but poorly understood aspect of sauropodomorph evolution concerns the extent to which different groups preferentially inhabited particular environments.

Previous analyses

Only a small number of studies have attempted to address the above question quantitatively, but these have presented analyses based on extensive datasets of sauropodomorph occurrences. For example, Lockley *et al*. (1994) used the trackway record to demonstrate that: (1) sauropods often walked on submerged substrates in coastal and deltaic settings; (2) tracksites are mainly associated with tropical and

subtropical latitudes (mean average Northern Hemisphere palaeolatitude = 25°); and (3) the majority of trackways occur in semi-arid or seasonal climatic environments where carbonate deposition was taking place (i.e. in lacustrine settings or in marine carbonate platform environments). The only other quantitative analyses of sauropod environmental associations have been undertaken by Butler *et al*. (2007) and Butler and Barrett (2008), based on an extensive dataset of Cretaceous dinosaurs. Butler and Barrett (2008, p. 1030-1031) wrote:

'Lockley *et al*. (1994) demonstrated, on the basis of a whole Mesozoic dataset, that sauropod ichnofossils are strongly associated with low-latitude carbonate deposits, in either coastal carbonate platform settings or lacustrine environments. Our database partially confirms this result: 32% of the Cretaceous sauropod ichnological record is found in coastal environments, as compared to only 7% of the Cretaceous sauropod body fossil record. However, our statistical analysis of the ichnological data does not find that sauropod trackways are overrepresented in coastal environments relative to trackways of other herbivorous groups. Analysis of the total-evidence dataset recovers a positive association between sauropods and terrestrial environments, which supports previous hypotheses of inland environmental preferences for the clade (e.g. Lehman 1987; Hunt *et al*. 1994). Therefore, body fossil evidence suggests more distal, or inland (away from channels), palaeoenvironmental preferences for sauropods, at least during the Cretaceous, when compared to contemporaneous clades such as Nodosauridae and Hadrosauridae. Sauropod footprints indicate that sauropods undoubtedly did enter coastal palaeoenvironments on occasion - preservation potential for footprints in coastal environments may have been higher than in contemporaneous inland habitats.'

Thus, both Lockley *et al*. (1994) and Butler and Barrett (2008) focused on the environments occupied by sauropods as a whole, with discussion of 'within sauropod' patterns limited to the distributions of Macronaria versus non-Macronaria. Butler *et al*. (2007, p. 54-55) noted that 'Sauropods show little evidence for broad environmental

associations: a significant negative association between Macronaria and coastal environments may be a result of taphonomic processes.' and recorded a positive association between Macronaria and inland environments (Butler and Barrett [2008]: table 1; $p < 1x10^{-4}$).

Discussion

While Lockley *et al*. (1994) found a strong association between sauropod tracksites and coastal environments, the analysis of Butler and Barrett (2008) recovered no support for sauropods being overrepresented in coastal environments when compared to other herbivorous dinosaurs, and in fact found evidence for a preference for inland settings. However, it is worth bearing in mind the limitations of both studies: Lockley *et al*. (1994) were restricted to a dataset of sauropod tracksites, while Butler and Barrett (2008) only considered the Cretaceous record of sauropods. As such, the entire Jurassic body fossil record has been excluded from previous environmental analyses. This exclusion may have resulted in erroneous results; for example, it is possible that groups of sauropods not present in the Cretaceous (e.g. non-neosauropod eusauropods and flagellicaudatans) showed a different environmental preference to Cretaceous forms (largely dominated by titanosauriforms). As such, use of a complete Mesozoic dataset may reveal previously unreported environmental patterns and could demonstrate niche separation between sauropod clades as well as temporal fluctuations. The methods applied by Butler and Barrett (2008; i.e. chi-squared tests) are appropriate, but consideration of different taxonomic groupings, as well as time binning the data (in addition to analysing it in its entirety), may allow a more refined study.

Review of previous dinosaurian distribution, diversity and completeness studies

Introduction

Deducing diversity patterns through time is an important element in understanding the macroevolutionary history of a group of organisms. The recovery of peaks and troughs in the diversity curve, and knowledge of their magnitude and sequence, enables us to assess the tempo and mode of evolution in any clade, as well as recognise major events in the history of life, including adaptive radiations and extinctions (Valentine 1985; Jablonski *et al*. 1996; Jablonski 2005). In addition, detailed knowledge of these patterns allows testing of potentially important evolutionary processes, such as competition and co-evolution (e.g. Bakker 1978; Vermeij 1983; Collinson and Hooker 1991; Benton 1996; Barrett and Upchurch 2005; Butler *et al*. 2009a, b, c), over extended temporal scales. There are several ways in which palaeobiodiversity can be defined and thus measured (Smith 1994); here, diversity refers to the number of taxa (e.g. species, genera, etc.).

There have been a number of large-scale studies of dinosaur diversity (Dodson 1990; Haubold 1990; Dodson and Dawson 1991; Sereno 1997, 1999; Fastovsky *et al*. 2004; Taylor 2006; Wang and Dodson 2006; Carrano 2008a; Lloyd *et al*. 2008; Barrett *et al*. 2009), while there have also been several analyses investigating the diversity of particular clades of dinosaurs (Hunt *et al*. 1994; Lockley *et al*. 1994; Weishampel and Jianu 2000; Barrett and Willis 2001; Barrett and Upchurch 2005; Upchurch and Barrett 2005; Mannion 2009b). The majority of these studies were based on taxonomic diversity records (i.e. direct readings of the fossil record by counting the numbers of genera or families that can be observed through geological time). Seven of these analyses (Sereno 1997, 1999; Weishampel and Jianu 2000; Upchurch and Barrett 2005; Lloyd *et al*. 2008; Barrett *et al*. 2009; Mannion 2009b) incorporated phylogenetic relationships into the diversity estimates. A second subset of studies (Fastovsky *et al*. 2004; Barrett and Upchurch 2005; Upchurch and Barrett 2005; Wang and Dodson 2006; Carrano 2008a;

Lloyd *et al*. 2008; Barrett *et al*. 2009; Mannion 2009b) have attempted to take into account sampling biases that might affect any reading of the dinosaur fossil record.

Dinosaur distribution

Global distribution

Weishampel *et al*. (2004a) collated data on all known occurrences of dinosaurs, including body fossils, eggs and tracksites. Localities were based on the primary administrative divisions (e.g. states, departments, provinces, counties) of the countries from which dinosaur remains have been discovered. The study showed that there has been a 55% increase in the number of known localities since the previous global study (Weishampel 1990), which demonstrates the growth in dinosaurian research in the last two decades. Not only has there been an increase in the number of localities, but previously under-represented high latitude regions (such as Antarctica and Australasia) are providing data as are less well-studied time periods (i.e. the Triassic, Early-Middle Jurassic and Early Cretaceous). There have also been increases across all the continents, particularly the Americas, Europe and Asia. The study summarised all known dinosaur locations (providing stratigraphic information) and also plotted the occurrences on to modern day maps for a number of time intervals.

Sauropod trackway distribution

Lockley *et al*. (1994) analysed a dataset of 438 individual sauropod trackways at 190 sites in 33 general geographic localities. They noted that they are mainly associated with tropical and subtropical latitudes (with the mean palaeolatitude being 25°) and that the majority of trackways occurred in semi-arid or seasonal climatic environments where carbonate deposition was taking place (i.e. in lacustrine settings or in marine carbonate platform environments). The authors also pointed out the absence of tracks in humid or

swampy settings and the rarity at high latitudes and in siliciclastic fluvial settings. Lockley *et al*. (1994) also demonstrated the correlation of sauropod tracksites with eustatic sea level (Haq *et al*. 1987), noting the high abundance of tracksites in the Oxfordian-Berriasian (a time of high sea level) and a lack of tracksites during the Valanginian (an interval of low sea level). Likewise, both the periods of high sea level of the Hauterivian-Barremian and Albian-Cenomanian correspond to high levels of abundance of sauropod tracksites. The authors explained this strong correlation non-biotically as a result of sauropod tracksites often occurring in paralic facies (i.e. during times of high sea level such deposits increase). Lastly, the authors compared the distribution of narrow-gauge (*Parabrontropodus*) and wide-gauge (*Brontopodus*) trackways through time, with their results demonstrating a transition from narrow-to-wide-gauge occurring during the Kimmeridgian-Tithonian.

Dinosaur distribution in the context of climate and vegetation

Rees *et al*. (2004) discussed the distribution patterns of Late Jurassic dinosaurs in the context of climate and vegetation. Taxic diversity was calculated by counting body fossils and tracksites within each dinosaur-bearing formation (using the dataset of Weishampel *et al*. 2004): eggs and coprolites were excluded from their analysis because of the difficulty in assigning these to particular genera or species based on body fossils. Fossils that could not be identified at the generic level were only counted as in a formation when a named representative of that group was not already present. Dinosaurs were demonstrated as being restricted to between approximately 50°N and 50°S of the palaeoequator (Fig. 1.5A). Rees *et al*. (2004) showed that dinosaur diversity is highest between 30-40°N and 30-40°S (Fig. 1.5A), although diversity is much higher in the Northern Hemisphere (though the authors suggested that this is probably due to sampling biases and a smaller land surface area in the Southern Hemisphere). Plant diversity (Fig. 1.5B) peaks slightly more poleward in the Northern Hemisphere, between 40-50°N, but at 30-40°S in the Southern Hemisphere (which is the same latitudinal

distribution as dinosaurs). However, plant diversity spans a much greater latitudinal range: up to 80°N and 70°S (Fig. 1.5B).

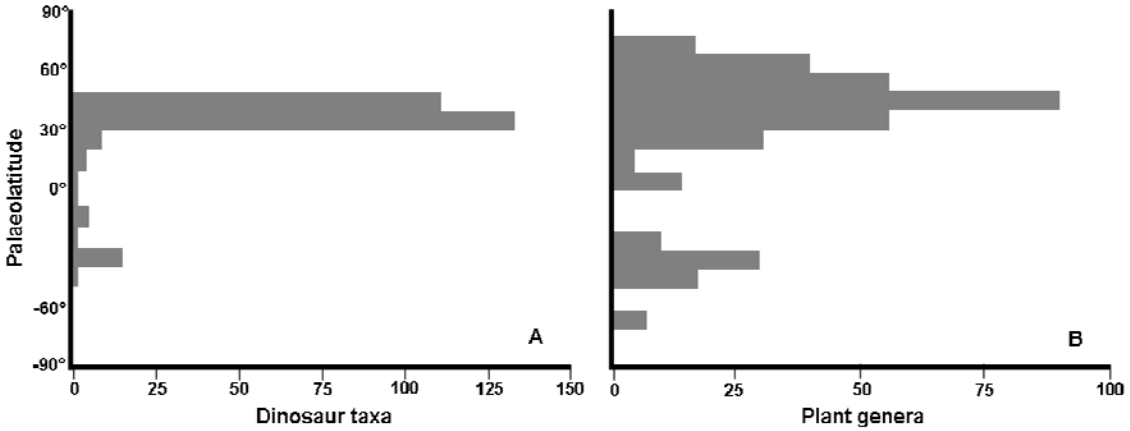

FIGURE 1.5. Distributions of (A) dinosaurian taxa and (B) plant genera in 10° palaeolatitudinal bins (after Rees *et al*. 2004).

Longitudinally, dinosaur diversity is greatest in Europe and North America, while plant diversity is highest in China, eastern Russia, India and Europe, with relatively low levels in the USA (Fig. 1.6). Rees *et al*. (2004) also noted that whereas there is an absence of dinosaurs at higher latitudes, there is an abundance of fossil floras and coals here (Fig. 1.6). At lower latitudes there is a co-occurrence of dinosaurs with evaporites and floras containing abundant microphyllous taxa (Fig. 1.6). However, the authors did consider the possibility that this may be the result of taphonomic biases, with dinosaurs missing from higher latitudes which were warm and wet (i.e. conditions which do not favour preservation). Rees *et al*. (2004, p. 643) suggested that 'dinosaur preservation was favored in environments toward the drier end of the climate spectrum, where savannas rather than forests predominated'.

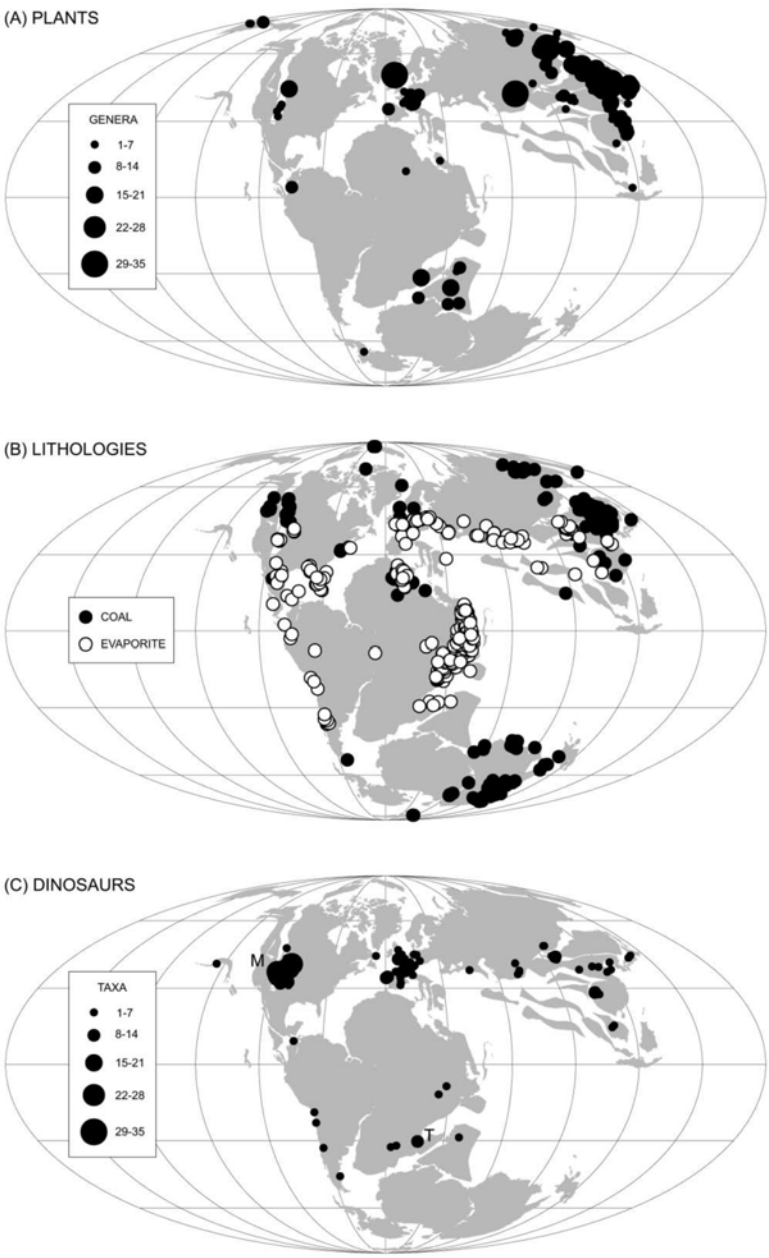

FIGURE 1.6. Late Jurassic (150 Ma) palaeogeographic maps (Mollweide projection with 30° latitude and longitude lines). (A) Plant localities, scaled according to the number of constituent genera, (B) Evaporite and coal deposits, (C) Dinosaur localities, scaled according to the number of constituent taxa and showing the location of the Morrison (M) and Tendaguru (T) Formations (after Rees *et al*. 2004).

Using the Morrison and Tendaguru ecosystems as case studies (Fig. 1.6C), Rees *et al*. (2004) noted that they both occur at similar palaeolatitudes but in different hemispheres. Both appear to have been semi-arid environments with large concentrations of herbivorous dinosaurs (mainly sauropods) and a high diversity of herbaceous and arborescent plants near bodies of water. They suggested that the differences in sauropods in the two deposits (Tendaguru is dominated by *Brachiosaurus* while the Morrison is dominated by diplodocids and *Camarasaurus*) may be due to differences in the structure of their plant communities.

Dinosaur diversity

Counting dinosaurs

Dodson (1990) stated that the fossil record of ornithischians (9.3 specimens per genus) is better than that of saurischians (6.2 specimens per genus), with certain dinosaurs being much more abundantly preserved than others (e.g. *Maiasaura*, *Psittacosaurus*, *Coelophysis* and *Plateosaurus*); however, he also noted that 45.3% of valid dinosaur genera are represented by only a single specimen. Dodson (1990) analysed the distribution of dinosaurs through time: he showed that the Kimmeridgian-Tithonian and Campanian-Maastrichtian include 12.6% and 39.3% of all known dinosaurs, respectively, in total comprising over 50% of all known dinosaur genera in less than 20% of the total time-span of the dinosaurs. Niklas *et al*. (1980) showed that North American Cretaceous outcrop area exceeds Jurassic outcrop area by a factor of nine, but North American Cretaceous dinosaur diversity is only 2.6 times greater than that for the Jurassic (Dodson 1990), suggesting that Cretaceous dinosaur diversity may be over-represented. However, the diversity of dinosaurs from the 1000 km^2 outcrop of the Campanian Judith River Formation of Alberta (Canada) exceeds the dinosaur diversity of the entire Kimmeridgian-Tithonian Morrison Formation that outcrops over 1,000,000 km^2 (Dodson 1990). Dodson (1990) also discussed the many biases that affect the fossil record,

including a historical bias: for example, 170 new genera were described between 1824 and 1969, but in just the following 20 years a further 115 genera were erected.

Using the assumption that a genus recorded in any one stage lasted for the entire stage, Dodson (1990) showed that the average longevity of a dinosaur genus is 7.7 Myr. He also calculated this only for those genera represented by more than one specimen (as a single specimen cannot have a temporal range), which yielded a longevity of 10.5 Myr per genus (however, this method has the problem of overestimating longevity through the omission of potentially legitimate single stage occurrences). Lastly, he carried out this analysis on a finer scale, looking at taxonomic turnover in formations within the same geographic region. Dodson (1990) found that the average longevity is approximately 4.2 Myr per genus in both Alberta and Mongolia (however, this method is problematic in that it may underestimate the longevity if the dinosaur originated earlier or survived elsewhere). Using these longevity estimates Dodson (1990) then attempted to calculate the number of dinosaur genera that ever lived (including those still to be discovered) using three different models of diversity. The first of these was based on a model of constant diversity (anchored on the Campanian-Maastrichtian) which Dodson (1990, p. 7610) rejected as 'not biologically reasonable'. The other two calculations used a model of increasing diversity and a bottleneck model, with the latter more closely matching the patterns of the fossil record. Using the estimates associated with the middle values for generic longevity (i.e. 7.7 Myr per genus), Dodson (1990) estimated that the number of dinosaurs that had ever lived were between 900-1200 genera.

In an update of Dodson (1990), Wang and Dodson (2006) made another endeavour to estimate dinosaurian diversity, including those that remain to be discovered. They used a statistical method called the abundance-based coverage estimator (ACE) to attempt to account for the incompleteness of the fossil record. The ACE method requires genera to be divided into groups of rare and abundant genera (with abundant genera being those represented by >10 individuals), with only the rare genera used to estimate diversity.

The use of only rare genera is for several reasons: (1) it is often difficult to determine the number of individuals in very large bonebeds; (2) finds of abundant genera that are already known are less likely to be collected or reported in the literature than a new genus; (3) 'undiscovered genera are inherently rare and would likely be represented by only a few individuals if discovered' (Wang and Dodson 2006, p. 13605). The ACE uses the number of known rare genera to estimate the total relative abundance of all known genera. By using the ACE, the authors estimated dinosaur diversity (including genera that remain to be discovered) at 1,844 genera, meaning that only 29% of all discoverable genera are currently known. Wang and Dodson (2006) also showed that since 1990 there has been an average of 14.8 genera described annually, compared with 5.8 genera from 1970-1986 and 1.1 genera from 1824-1969. Overall, there has been an 85% increase in named genera since 1990.

Taylor (2006) analysed apparent diversity in terms of the number of valid genera within each major clade, stratigraphic stage, place of discovery and year of description. His analysis by clade showed that Saurischia (300 genera) outnumbers Ornithischia (180 genera) by 66% and that theropods make up 59% of Saurischia and account for 36% of Dinosauria. Taylor's (2006) analysis by geological age showed that dinosaurian diversity generally increased throughout the Mesozoic, with 40 genera first appearing in the Triassic, 134 in the Jurassic and 310 in the Cretaceous (Fig. 1.7). Taylor (2006) then attempted to correct this by normalising the diversity by geological period duration; however the overall trend was the same: Triassic dinosaurs had a genus density (GD) of 1.84 genera per Myr, Jurassic dinosaurs had a GD of 2.18 and Cretaceous dinosaurs had a GD of 3.91. His analysis also demonstrated that 6 stages are the most productive for genera: Campanian (98 genera), Maastrichtian (44), Kimmeridgian (41), Albian (30), Aptian (25) and Barremian (25), with these 6 stages making up over half of all dinosaurian genera over a period of less than a third of their total existence (Fig. 1.7). The Kimmeridgian has a GD of 12.06, with the Campanian (7.84) and Maastrichtian (7.33) also being apparently highly diverse (Fig. 1.7). These three stages make up 38% of

dinosaurian genera in just over 13% of their existence and Taylor (2006) suggested that these three peaks reflected genuinely high levels of diversity rather than the effects of sampling biases. The author also tested for any correlation between diversity and sea level, finding only a weak correlation with genus counts ($r^2 = 0.208$) and an even weaker correlation with GD ($r^2 = 0.177$) (contra Haubold [1990] and Hunt *et al*. [1994]).

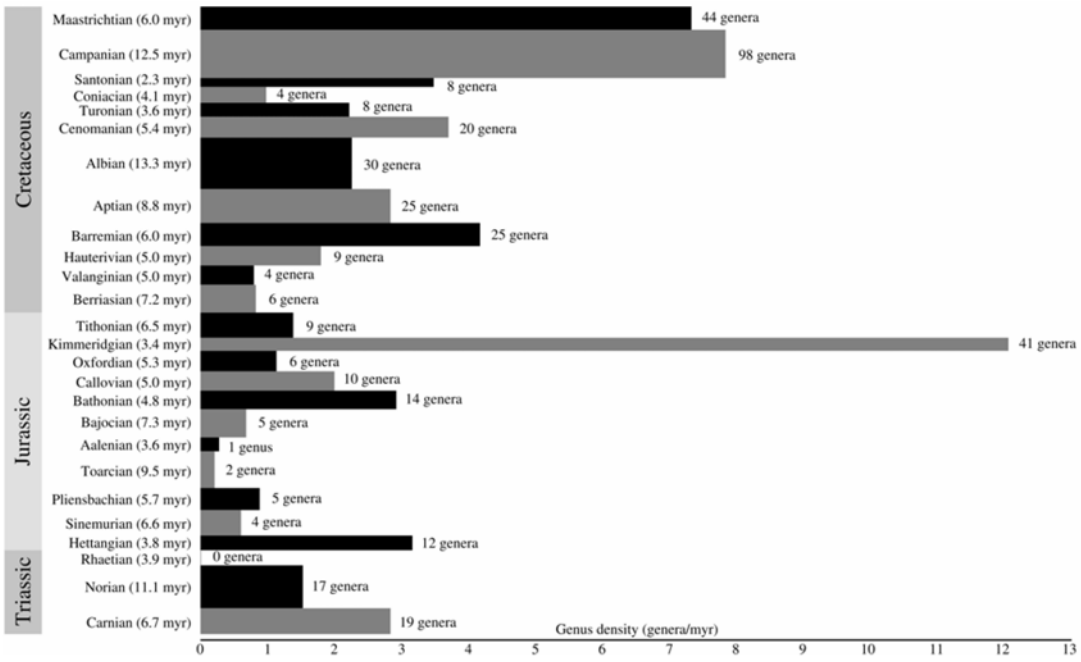

FIGURE 1.7. Dinosaur taxic diversity by stratigraphic stage (after Taylor 2006).

Taylor's (2006) analysis of genera by place demonstrated that six countries accounted for nearly 75% of all dinosaur diversity: USA (108 genera), China (80), Mongolia (59), Argentina (46), England (34) and Canada (32). Wang and Dodson (2006) found a similar pattern and noted that diversity had increased substantially in four of these countries since 1990: Argentina (+165%), China (+132%), USA (+48% increase) and Mongolia (+45%). Taylor (2006) also noted an increase in taxa named from the Southern Hemisphere in the last 90 years (up from 7.4% to 23%).

Diversity of Dinosauria

The earliest modern studies of dinosaur diversity focused on determining the raw numbers of dinosaur taxa present during the Mesozoic (Dodson 1990; Haubold 1990). These analyses agreed on a general pattern that included three diversity peaks (Late Triassic, Late Jurassic and Late Cretaceous), which were suggested to be at least partly tied to sea level cycles; however, they presented opposing views on the specific relationships between diversity and sea level. Both studies acknowledged the importance of sampling and other biases, but were unable to assess them quantitatively.

Sereno (1997, 1999) produced time-calibrated cladograms for all dinosaurs and used these to assess diversity. This early attempt to assess phylogenetic diversity confirmed that the appearance of basal ornithischians (heterodontosaurids) and basal sauropodomorphs ('prosauropods') in the Late Triassic resulted in a small diversity peak, with sauropod diversity reaching its apex in the Late Jurassic (Fig. 1.8). Overall dinosaur diversity was low in the earliest Cretaceous, followed by a general increase in the mid-Cretaceous and a large rise during the Campanian–Maastrichtian (Fig. 1.8): ceratopsians and ornithopods achieved their greatest diversity at this time (Sereno 1999). Although these two studies (Sereno 1997, 1999) took into account the effects of available rock outcrop area on diversity, peaks were considered as genuine biological events, while troughs in diversity were interpreted as sampling biases. Consequently, the resultant estimated diversity curve showed a gradual diversity increase during the Triassic–Jurassic, before a relatively rapid increase throughout the Cretaceous (Fig. 1.8). A similar pattern was recovered by Lloyd *et al*. (2008), who constructed a time-calibrated dinosaurian supertree which was used to estimate diversification rates across the clade.

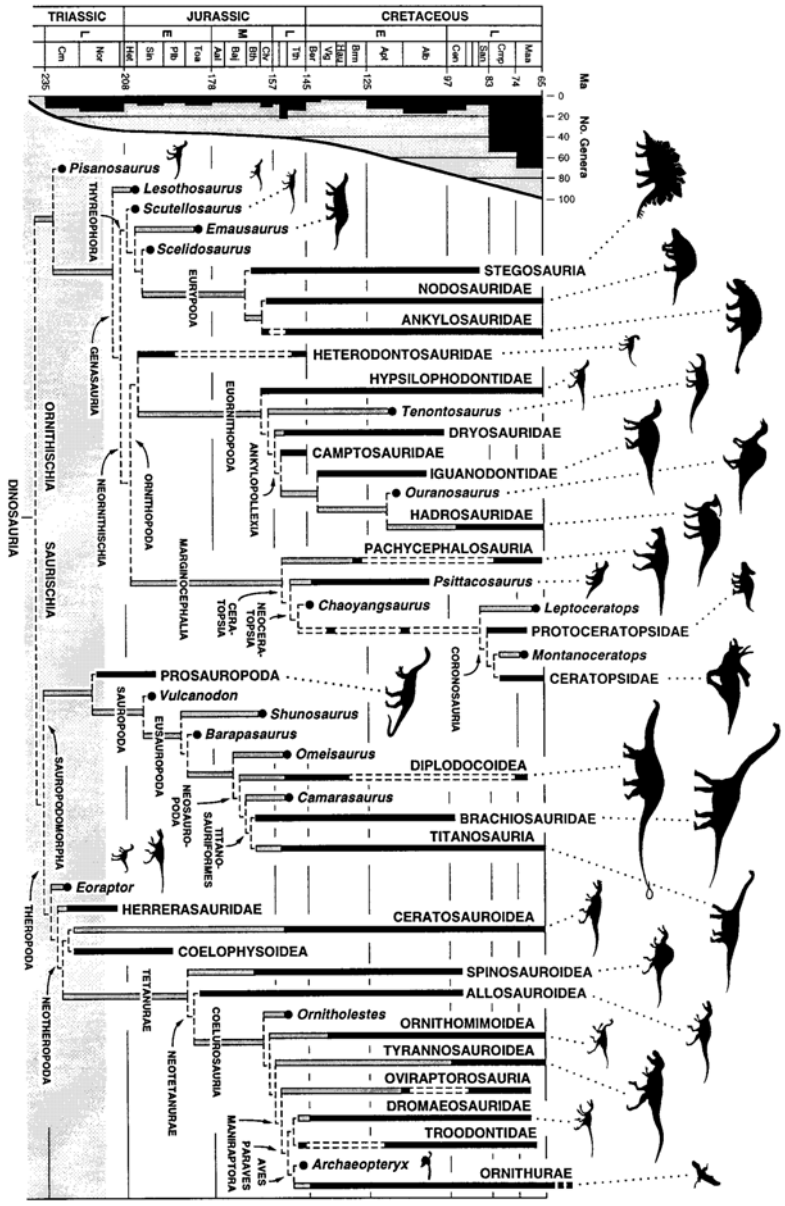

FIGURE 1.8. Temporally calibrated phylogeny of the Dinosauria, showing known temporal durations (solid bars), missing ranges (shaded bars), and ranges extended by fragmentary or undescribed specimens (dashed bars). At the top is a tabulated number of recorded nonavian dinosaurian genera per stage, as well as an estimated curve of generic diversity (after Sereno 1999).

Weishampel and Jianu (2000) analysed the diversity of herbivorous dinosaurs using both taxic and phylogenetic methods. They used composite cladograms for both Ornithischia and Sauropodomorpha (the latter clade is discussed in the following section), making them relatively comprehensive but at the cost of low resolution. The phylogenetic relationships were then calibrated against the earliest occurrence of each species. In an attempt to assess the relationship between estimates of ornithischian diversity and ghost lineages, they sampled at 2.5 Myr intervals (this time interval was chosen in view of Dodson's [1990] calculation that the temporal range of dinosaurian species is approximately 5 Myr). Their taxonomic diversity estimate (TDE) for Ornithischia (Fig. 1.9A) shows a peak in the Early Jurassic, followed by a series of larger peaks in the Late Jurassic. There is also a peak at the end of the Early Cretaceous with the largest peak at the end-Cretaceous. Their phylogenetic diversity estimate (PDE) for Ornithischia (Fig. 1.9B), in contrast, shows a more gradual rise in diversity from the Early to Late Jurassic at which point there was an abrupt increase. This was then followed by a series of small peaks and troughs, before diversity reached its zenith in the latest Cretaceous.

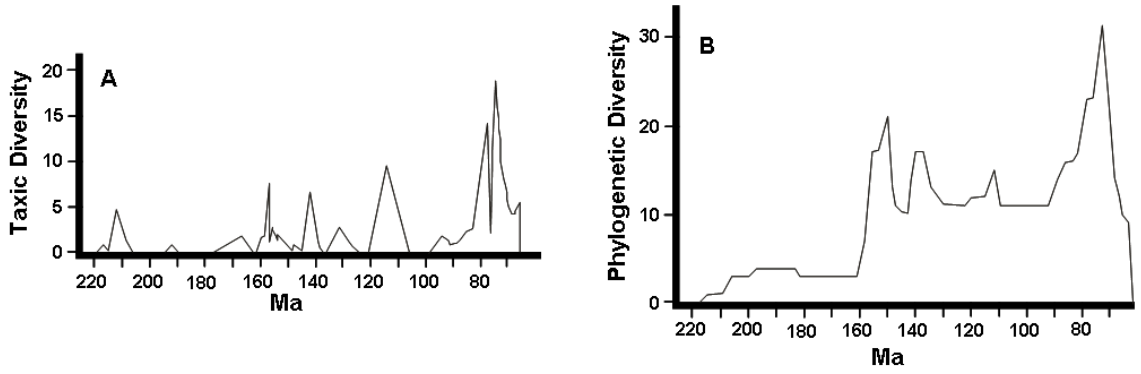

FIGURE 1.9. Ornithischian diversity through the Mesozoic based on (A) taxic and (B) phylogenetic diversity estimates (after Weishampel and Jianu 2000).

Thus far, only one published study has implemented rarefaction in an attempt to elucidate dinosaur diversity: Fastovsky *et al*. (2004) utilised the global dinosaur locality dataset of Weishampel *et al*. (2004b), pruning it to exclude generically indeterminate

material. These authors demonstrated a steady increase in diversity throughout the Mesozoic (Fig. 1.10) and argued that dinosaurs were not in decline in the last 10 Myr of the Mesozoic (Fig. 1.11). This study has been criticised by several workers (Archibald 2005; MacLeod and Archibald 2005; Sullivan 2006), who questioned the interpretation of the rarefied data by Fastovsky *et al*. (2004) and suggested (after re-analysis) that a Maastrichtian decline in dinosaur diversity is still well supported (Barrett *et al*. [2009] also recovered support for this decline). However, Carrano (2008a) demonstrated that dinosaur diversity for the latest Cretaceous of North America shows much less variation between formations and time intervals than is documented by stage level diversity counts and suggested that, rather than reflecting an end-Cretaceous decline, Campanian–Maastrichtian fluctuations (at least for North America) are the product of ecological, environmental and sampling biases (particularly of an anthropogenic nature).

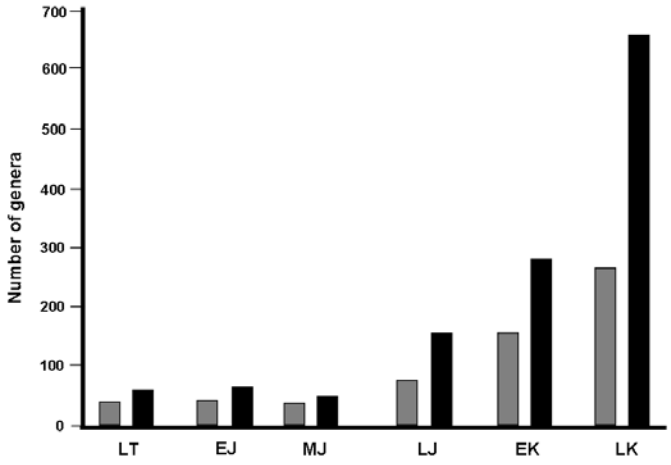

FIGURE 1.10. Dinosaur generic richness through Mesozoic by epoch. Each epoch has two metrics: absolute generic richness (grey bars), which consists of summation of different genera found during that time interval, and total sample counts (black bars), which consists of numbers dinosaur bearing localities (after Fastovsky *et al*. 2004).

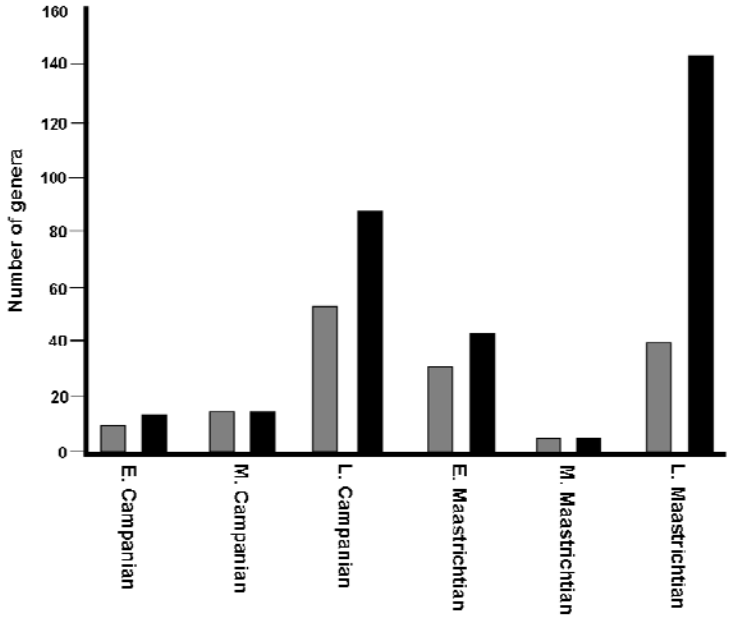

FIGURE 1.11. Dinosaur generic richness through the latest Cretaceous by substage. Each substage has two metrics: absolute generic richness (grey bars), which consists of summation of different genera found during that time interval, and total sample counts (black bars) (after Fastovsky *et al*. 2004).

Wang and Dodson (2006) used their ACE method (see 'Counting dinosaurs' above) to look at dinosaurian diversity in each epoch: this showed a general increase in diversity through time, with the largest peak in the Late Cretaceous, while the Middle Jurassic had the lowest percentage of known genera (20%). The authors also looked at whether there was already a decline in dinosaur diversity before the end-Cretaceous, as 86 'well resolved' genera are known from the Campanian and 76 from the Maastrichtian (including 16 known from both stages), suggesting a diversity decline (Fig. 1.12). However, the ACE yielded a diversity of 209 genera in the Campanian and 213 genera in the Maastrichtian, using only 'well resolved' genera. They then also randomly assigned Late Cretaceous 'poorly resolved' genera into individual stages and carried out 100 sets of randomization tests, resulting in an average diversity of 245.9 genera in the Campanian and 246.3 genera in the Maastrichtian, again suggesting that there was no

decline (Fig. 1.12). Wang and Dodson (2006) also suggested that the Campanian dinosaur record is much more complete than that of the Maastrichtian, although the authors noted that it is possible that there was a gradual decline during the Maastrichtian (rather than between the Campanian and the Maastrichtian) instead.

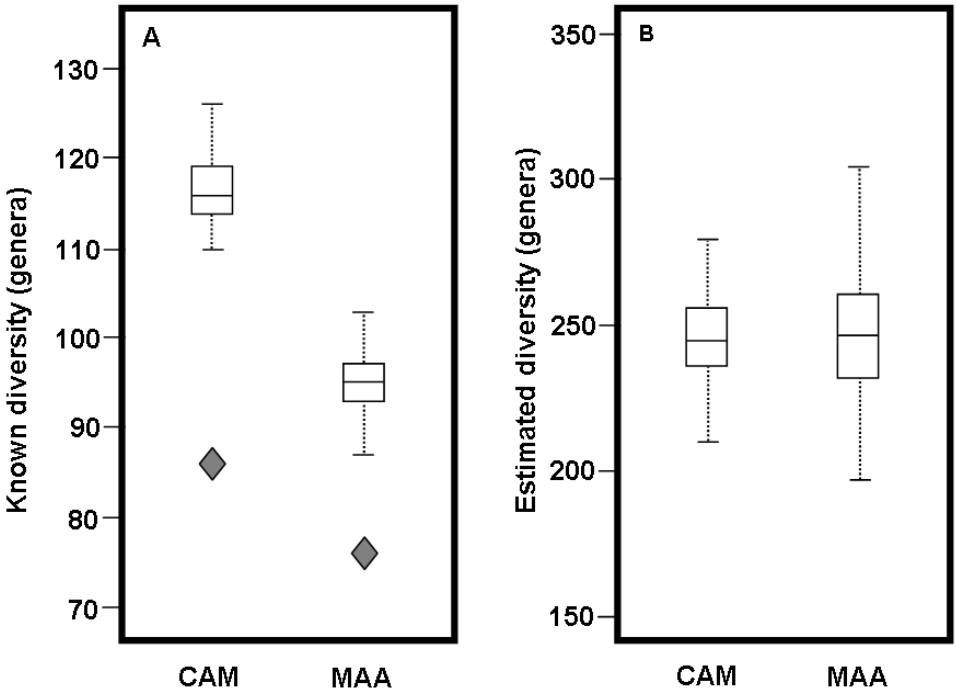

FIGURE 1.12. (A) Known and (B) estimated diversity in the last two Late Cretaceous stages. The number of well-resolved genera known from each stage is marked by a gray diamond. Box plots show middle 50% of values with the median shown as a horizontal line within the box (after Wang and Dodson 2006).

Wang and Dodson (2006) also looked at bias in diversity due to rock availability (Fig. 1.13). They used epoch level data on the number of formations in the United States (Peters and Foote 2001) and found that known diversity (Fig. 1.13A) is strongly correlated with the number of formations during the Mesozoic (r^2 = 60.3%), but that the correlation between estimated diversity (Fig. 1.13B) and number of formations is much

lower (r^2 = 12.8%). They predicted that as the completeness of the dinosaur record improves, known diversity will become less correlated with rock availability.

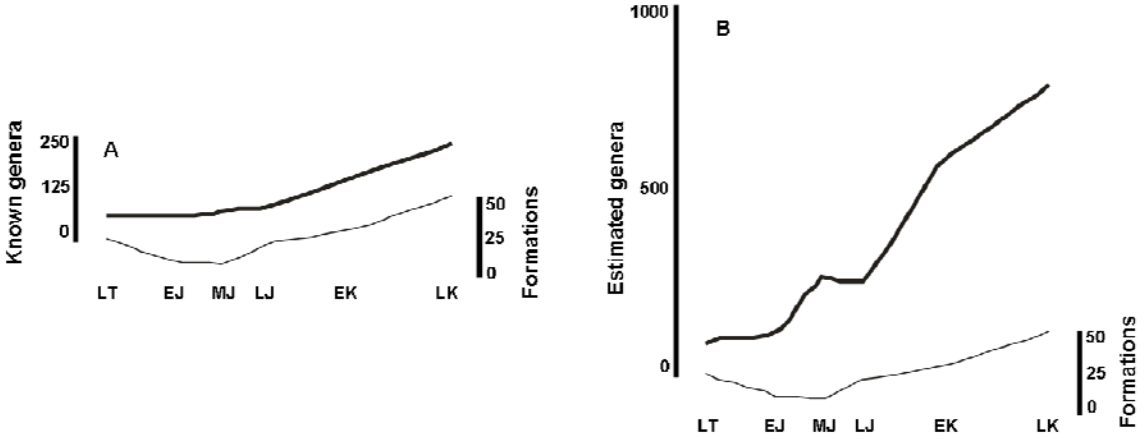

FIGURE 1.13. Relationship of (A) known and (B) estimated diversity (thick lines) with rock availability (thin lines). The number of terrestrial U.S. Geological Survey formations is used as a proxy for rock availability (after Wang and Dodson 2006).

Barrett *et al*. (2009) assessed dinosaur diversity (including Mesozoic birds) based on taxic and phylogenetic curves for genera and species. In order to test whether geological sampling biases impacted the shapes of these curves, these authors constructed a diversity model utilising the residuals method of Smith and McGowan (2007: see 'Materials and Methods'). This model predicted the expected genus richness for each dinosaur clade using the number of dinosaur-bearing formations (DBFs). Statistical comparisons between these models and the observed diversity curves suggested that ornithischian and theropod diversity patterns were significantly correlated with fluctuations in the rock record (as also suggested by Weishampel and Jianu [2000] and Upchurch and Barrett [2005]). However, sauropodomorph diversity was largely independent of changes in the number of DBFs, potentially resulting from genuine evolutionary events (Barrett *et al*. 2009; see also Upchurch and Barrett 2005).

Sauropodomorph diversity

Previous sauropodomorph diversity studies have tended to be part of either an overall study on dinosaur evolution (Bakker 1977, 1978; Sereno 1997, 1999) or an analysis of the factors controlling dinosaur diversity (Horner 1983; Weishampel and Horner 1987; Haubold 1990; Barrett and Willis 2001; Lloyd *et al*. 2008). These studies (with the exception of the work of Lloyd *et al*. 2008, which utilised a supertree), as well as the sauropod analysis of Hunt *et al*. (1994), were all based on taxic diversity counts and the overall consensus from these analyses was that sauropod diversity gradually increased throughout the Jurassic (reaching a peak at the Kimmeridgian-Tithonian), followed by a major extinction event at the Jurassic/Cretaceous (J/K) boundary, before a subsequent Late Cretaceous rise in diversity. The analyses of Hunt *et al*. (1994) and Barrett and Willis (2001), however, used larger datasets which enabled them to detect fluctuations on a finer scale. These latter studies noted diversity peaks in the Middle Jurassic (Bajocian), Late Jurassic (Kimmeridgian), Early Cretaceous (Valanginian-Barremian), mid-Cretaceous (Albian) and Late Cretaceous (Campanian-Maastrichtian). Haubold (1990) and Hunt *et al*. (1994) also recognised a number of correlations between these fluctuations in diversity and changes in sea level, which will be discussed in a later section.

Weishampel and Jianu (2000) studied sauropodomorph diversity using both taxic and phylogenetic methods. Their TDE shows a peak in the Late Jurassic, a smaller peak in the mid-Cretaceous and another near the end-Cretaceous (Fig. 1.14A). Their PDE shows a small peak at the end Triassic and another, slightly higher peak, at the start of the Jurassic; this is followed by a decline throughout the Early Jurassic, then a peak in the Middle Jurassic (contra to the authors' own interpretation), before the greatest peak at the end-Jurassic (Fig. 1.14B). There is then a gradual decline throughout the Cretaceous, though with a slight increase near the end-Cretaceous (Fig. 1.14B). There is very little correspondence between the TDE and PDE. Their data show a much higher

sauropodomorph diversity peak in the Middle Jurassic than had been previously estimated (about 75% of the diversity estimate for the Late Jurassic).

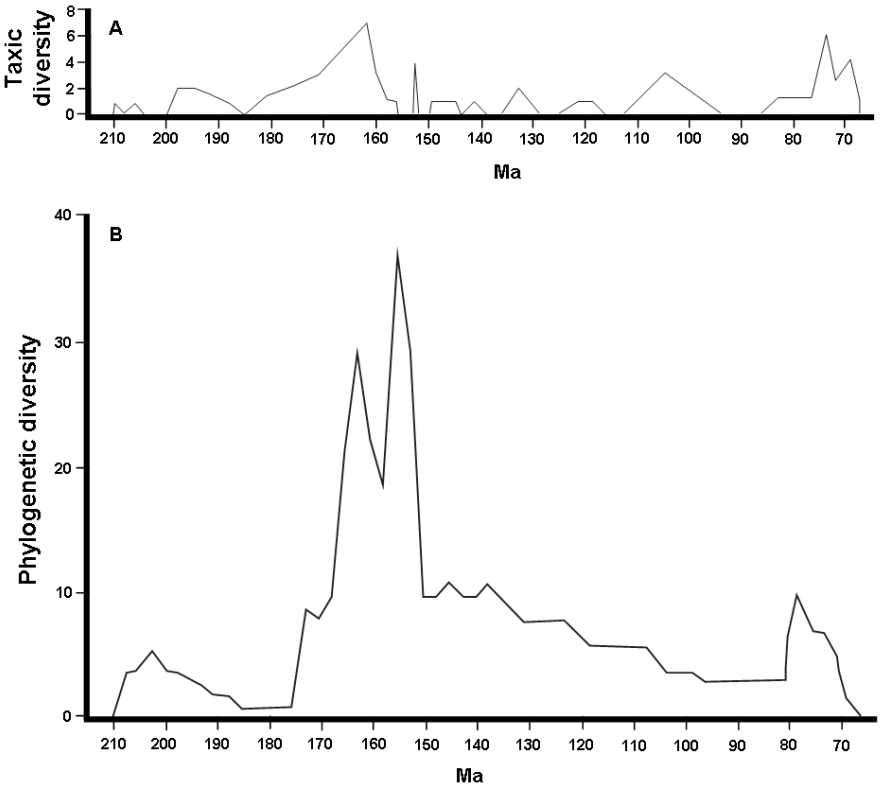

FIGURE 1.14. Sauropodomorph diversity through the Mesozoic, based on taxic (above) and phylogenetic (below) estimates (after Weishampel and Jianu 2000).

Upchurch and Barrett (2005) analysed sauropod diversity using both taxic and phylogenetic methods, though (unlike Weishampel and Jianu [2000]) they based the latter on the single cladogram of Upchurch *et al*. (2004). They compared their phylogenetic diversity curve with that of Weishampel and Jianu (2000); although the two curves are largely in close agreement, there are a few subtle differences: the main ones being the Middle Jurassic increase in sauropod diversity occurring slightly earlier and the diversity decline near the Jurassic/Cretaceous boundary occurring a little later in the Upchurch and Barrett (2005) study.

Upchurch and Barrett (2005) also compared their own taxic and phylogenetic diversity curves and utilised a rock record proxy in terms of number of 'dinosaur bearing formations' (DBFs). Both taxic and phylogenetic diversity curves agreed on many aspects of sauropod diversity but there were also several discrepancies (Fig. 1.15). Both show a noticeable increase leading into the Early Jurassic with a slight decline until the Toarcian, followed by a sudden increase in the Middle Jurassic. The PDE, however, is five times higher than the TDE, but this is probably largely a consequence of the inaccuracy of the dating and relationships of the problematic taxon *Bellusaurus* (Upchurch *et al*. 2004a; Upchurch and Barrett 2005). The authors suggested that this increase is probably a genuine signal as the major neosauropod lineages had already radiated by the Bathonian. Both curves indicate a dramatic drop during the Oxfordian, yet the number of DBFs reaches its Jurassic peak at this time (Fig. 1.15), again suggesting that this is a real signal. The Kimmeridgian-Tithonian is supported by both curves as the peak of sauropod diversity and the reduced number of DBFs (compared to the Oxfordian) suggests that this is again a real peak. Both the TDE and PDE curves show a large decrease across the J/K boundary; this is despite a considerable increase in the number of DBFs (Fig. 1.15). There are discrepancies in the two curves in the mid-Cretaceous (in the Albian the TDE values are 2.75 times higher than the PDEs); this is partly an issue of certain taxa being left out of the cladistic analysis, but is also probably related to a sampling bias with the number of DBFs greater during the Aptian-Albian than before or after, suggesting a relatively constant diversity from the Berriasian to Albian, before a decrease in the Cenomanian. Both diversity curves and the number of DBFs are relatively low between the Turonian-Coniacian; however, although partly a result of sampling bias, the number of DBFs is actually higher than during the Middle Jurassic, so diversity probably was low at this point (Fig. 1.15). An increase in both curves during the Santonian-Maastrichtian is a result of the titanosaur radiation (Upchurch and Barrett 2005); there is a close correspondence between fluctuations in both curves and the number of DBFs but relative to the rest of the Cretaceous the number of DBFs is only

moderately increased, suggesting the Campanian signal is at least partly genuine. The diversity curves also show a decline leading up to the K/P extinction (Fig. 1.15).

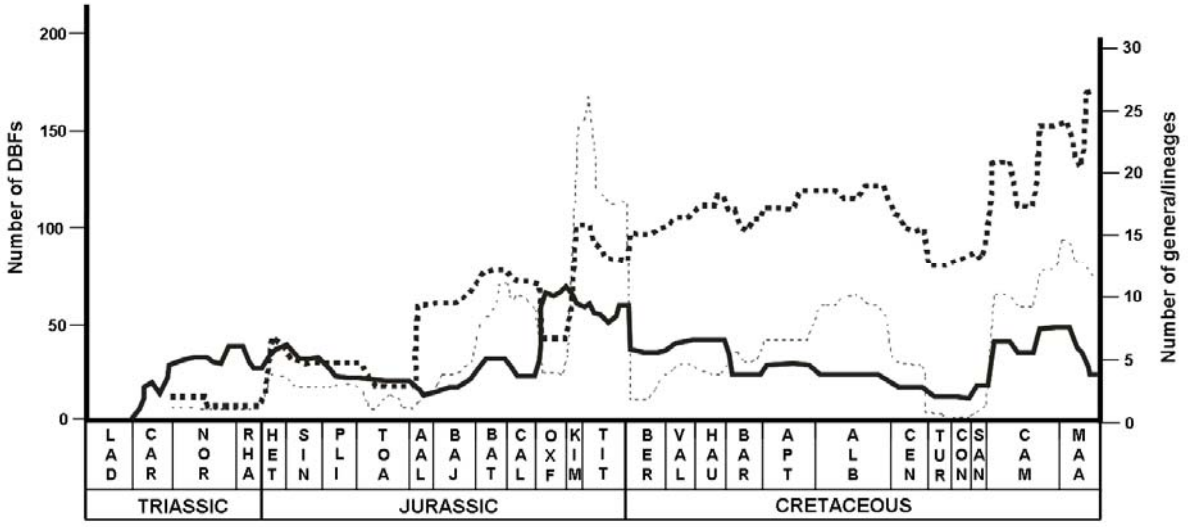

FIGURE 1.15. Comparison of taxic (black solid line) and phylogenetic (fine dashed line) diversity estimates for sauropod genera and number of dinosaur-bearing formations (thick dashed line) (after Upchurch and Barrett 2005).

Four of the five diversity peaks (Bajocian, Kimmeridgian, Valanginian-Barremian, and Campanian-Maastrichtian) identified by Haubold (1990) and Hunt *et al*. (1994) as correlating with high sea level were observed in the PDEs of Upchurch and Barrett (2005) and two of the four diversity troughs correlated with low sea level (Oxfordian and Turonian-Coniacian) were also visible. This suggests that these six intervals, at least, may potentially represent genuine (i.e. biotic) diversity signals rather than purely effects of taphonomic biases (see 'Materials and Methods' for a detailed discussion of the potential effects of sea level on diversity.

Barrett and Upchurch (2005) expanded the sauropod diversity analysis of Upchurch and Barrett (2005) to look at prosauropods, though they only analysed taxic diversity. Their results demonstrated a rapid radiation of prosauropods during the Norian, following

their first appearance in the middle Carnian (Fig. 1.16). There is then a subsequent drop in the Rhaetian before an apparent prominent increase in the Early Jurassic. From the middle Sinemurian onwards there is then a stepwise decrease in prosauropod diversity, before their probable extinction at the end of the Pliensbachian (Fig. 1.16). It should be noted that this work was based on the assumption that Prosauropoda is monophyletic; if prosauropods are a paraphyletic assemblage (Yates 2003a, 2004, 2007) then this may merely be a pseudo-extinction caused by a taxonomic artefact (Forey *et al*. 2004). Barrett and Upchurch (2005) also acknowledged the uncertainties involved in the dating of several genera and suggested that the Rhaetian diversity trough may reflect a taphonomic bias, based on a low number of DBFs during this stage (Fig. 1.16).

Most recently, Barrett *et al*. (2009) combined the 'prosauropod' and sauropod phylogenies of Galton and Upchurch (2004) and Upchurch *et al*. (2004a), respectively, to look at sauropodomorph diversity. Their diversity curves from the Middle Jurassic onwards are thus essentially the same as in Upchurch and Barrett (2005) and their Late Triassic diversity mirrors that of Barrett and Upchurch (2005). Only in the Early Jurassic is diversity shown to differ from these previous analyses: this is a consequence of the co-occurrence of basal sauropodomorphs, 'prosauropods' and sauropods. Sauropodomorph diversity is shown to have been high in the Hettangian-Pliensbachian (albeit with a minor drop in the TDE in the Sinemurian) before a notable decline in the Toarcian. Barrett *et al*. (2009) also compared their diversity curves with DBFs, but recovered extremely weak correlations.

Lastly, Barrett and Upchurch (2005) also analysed the diversity of feeding mechanisms within Sauropoda and looked for evidence of competitive replacements (both within Sauropodomorpha and in comparison with Ornithischia). Most 'candidate competitive replacements' (Benton 1996) within sauropods were shown to be unsupported by their analyses, with only one being weakly supported (the replacement of rebbachisaurids by titanosaurs in the mid-Late Cretaceous). Stronger evidence, though, was found for

sauropods potentially outcompeting prosauropods in the Early Jurassic. Barrett and Upchurch (2005) found a strong positive correlation between sauropod diversity and feeding ecology, suggesting that the evolution of different feeding strategies (which would also have allowed niche partitioning) was crucial to their radiation in the Middle-Late Jurassic.

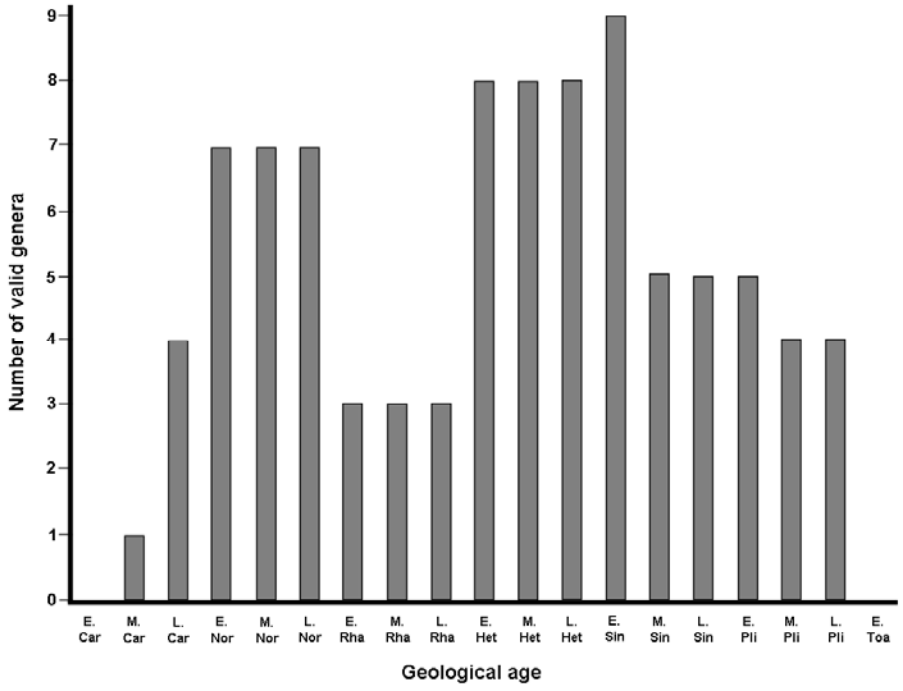

FIGURE 1.16. Taxic diversity estimates for the Prosauropoda (after Barrett and Upchurch 2005).

Dinosaur completeness

Completeness is a measure of how much of a taxon or specimen is known. Completeness metrics can be used to help address issues of fossil record quality (Fountaine *et al*. 2005) as well as historical patterns pertaining to taxonomy and nomenclature (Benton 2008a, b). They also may prove useful as sampling proxies in diversity studies.

Fountaine *et al*. (2005) used a relatively simple method for determining completeness in an attempt to assess the quality of the fossil record of Mesozoic birds. They split the number of birds per stratigraphic stage into those species known from (1) one bone, (2) more than one bone, (3) a partial skeleton, and (4) more than one partial skeleton. Their results showed that only the Maastrichtian is characterized by a seeming overabundance of fragmentary material, although it should be noted that this stage contained nearly three times as many species as the next most diverse stage (the Campanian).

Benton (2008a, b) investigated how taxonomic error rate (the number of synonyms and other erroneous taxa divided by the total number of named taxa) in dinosaurs (including Mesozoic birds) has changed through historical time. Benton (2008a, b) showed that the taxonomic error rate has decreased towards the present day, particularly over the past 15 years. He hypothesized that this trend partly reflects a reduction in revision time, but has occurred mainly because modern workers base their new taxa on more complete type specimens (Benton 2008b). Benton tested this hypothesis by estimating the quality of type specimens using a completeness score ranging from 1 to 5, where: 1 = isolated teeth or bones, 2 = one complete or near-complete skull, 3 = several skulls, 4 = one complete or near-complete skeleton, and 5 = several skeletons. One analysis (Benton 2008b) sampled just over 100 dinosaurian genera from six 5-year time bins (i.e. 1840-1844, 1870-1874, 1900-1904, 1925-1929, 1950-1954, 1975-1979) and showed that the ratio of type specimens with completeness scores of 2-5 to those with scores of 1 has increased through time, especially recently. A comprehensive study of over 1,000 dinosaurian genera (Benton 2008a) examined the ratio of good to poor type specimens, where ‘good’ type material was defined as a complete or partial skull and/or skeleton, where ‘partial’ meant that at least 50% of the skull or skeleton was preserved, and ‘poor’ type material was defined as ‘anything from a single tooth to a collection of 10 or 15 isolated elements from different regions of the skull and skeleton’ (Benton 2008a, p.

2). Again, when this ratio is calculated for each of the ten-year time bins between 1824 and 2004 there is a trend towards increasing quality of type material through time.

Discussion

The overall consensus from previous analyses of sauropodomorph diversity is that species richness was high during the Norian, Bajocian-Callovian, Kimmeridgian-Tithonian, Albian and Campanian-Maastrichtian (with possibly a small peak in the Valanginian-Hauterivian too), with depauperate faunas present during the Rhaetian, Toarcian-Aalenian, Oxfordian, Berriasian and Turonian-Coniacian. However, Upchurch and Barrett (2005) proposed that the Toarcian-Aalenian, Berriasian and Albian diversity levels are partly the product of taphonomic artefacts, resulting from fluctuations in the number of opportunities to observe (NOOs), although only the Albian peak appears to be entirely dependant on NOOs (Barrett *et al*. 2009).

Currently, sauropodomorph diversity has only been analysed for taxa named before 2004 and using phylogenies from no later than this; as such, utilising more recent phylogenies (i.e. Upchurch *et al*. 2007a; Yates 2007) and taxa named in the intervening years will improve any diversity analysis. Additionally, there is the potential to use more than just DBFs for analysing the effects of sampling biases on sauropodomorph genus richness. Other proxies that could be compared with diversity include sea level (which has been proposed by previous authors to exert a control [see above]) and numbers of dinosaur collections (Carrano 2008b; www.paleodb.org). Completeness of taxa, using a modified version of the metrics used by Fountaine *et al*. (2005) and Benton (2008a, b), may also prove to be a useful proxy for the rock record. As well as directly comparing these proxies with diversity, the residuals method of Smith and McGowan (2007) could also be applied, as well as rarefaction (see 'Materials and Methods'). Sauropodomorphs make a particularly useful case study as, unlike the other dinosaurian clades, previous

studies have suggested much of their diversity represents a genuine biological signal (Weishampel and Jianu 2000; Upchurch and Barrett 2005; Barrett *et al*. 2009).

Lastly, little effort has been applied to whether dinosaurs might demonstrate palaeolatitudinal preferences. Lockley *et al*. (1994) noted that the mean palaeolatitude for sauropods in the Northern Hemisphere was 25° (though this was based only on tracksites) and Butler and Barrett (2008) highlighted the possibility of some sort of habitat separation between sauropods and ornithischians during the Cretaceous (and it has been suggested before that there may have been niche separation between different sauropodomorph clades; see Barrett and Upchurch [2005]). However, neither of these studies examined this issue in any detail; thus, there is potential for consideration of this on a larger scale, i.e. by taking into account body fossils and tracksites for the entire Mesozoic.

Review of previous taphonomic studies of vertebrates

Introduction to taphonomy

In his seminal paper, Efremov (1940, p.85), in reference to palaeontology, stated that:

'The chief problem of this branch of science is the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere, i.e., the study of a process in the upshot of which the organisms pass out of the different parts of the biosphere and, being fossilized, become part of the lithosphere.'

He suggested (p. 88-89) that one of the key elements in understanding the fossil record would be:

'…the study of geological processes of the transition of animal remains from the biosphere into the lithosphere, and in the first place, the detailed study of the localities where a terrestrial fauna is found.'

To implement this, Efremov (1940, p. 89-90) highlighted the need for:

'The study of the processes of fossilization of animal remains. Microscopical and chemical analyses of fossilized remains, conducted together with experimental work of artificial fossilization, and with observations of the destruction of the surfaces of organic remains in different surroundings. The study of the processes of rounding off of the bones during transportation and the calculation for each locality of the relations between the rounded off bones and the object as a whole….To these problems can yet be added the study of pathological changings and damages in skeleton parts and the search for tokens of great episootical illnesses; here can be found an answer to the separate causes of the destruction of animals and the formation of accumulations of

remains appertaining to one species. The investigations indicated above make it possible to ascertain the condition of animal remains before fossilization, i.e., to explain the primary stages of the process of embedding and to investigate the process of destroying of animal remains before fossilization, and while it lasted.'

He also advocated using modern faunas as analogues to help understand the fossil record and concluded with a new name for this discipline of palaeontology (p. 93):

'I propose for this part of paleontology the name of 'TAPHONOMY', the science of the laws of embedding. I find that this new name will best reflect the chief direction of work in this new branch of paleontology.'

Taphonomy (from the Greek *taphos*, meaning burial, and *nomos,* meaning law) is the study of all factors (biotic and abiotic) that affect an organism after death. It is 'the study of processes of preservation and how they affect information in the fossil record' (Behrensmeyer and Kidwell 1985, p. 105). These processes remove or modify information about the organisms (e.g. through the loss of soft tissues or by transportation of the carcass), creating taphonomic biases. The primary motivation behind the study of taphonomy, thus, is to better understand these biases in the fossil record.

As well as being used to study individual specimens or a particular bonebed or regional assemblage (e.g. Hill and Behrensmeyer 1984; Dodson *et al*. 1980a, b; Sander 1992; Hungerbühler 1998; Winkler *et al*. 2000; Winkler and Rose 2006; González Riga and Astini 2007), taphonomy can also be used to explore 'megabiases', i.e. large-scale (both at a spatial and temporal level) patterns in the quality of the fossil record (Behrensmeyer *et al*. 2000).

Although many taphonomic studies are descriptive and/or quantitative analyses of particular assemblages, there are also numerous studies which have attempted to distinguish sampling biases from biotic factors. These include assumptions of random preservation and 'hollow curve' models for original taxonomic abundance as well as models that test the effects of incomplete fossilisation, stratigraphic incompleteness, nonrandom distributions of facies and hiatuses, and the effects of time-averaging (Marshall 1990, 1994; Gilinsky and Bennington 1994; Foote 1996; Foote and Raup 1996; Wagner 2000; Kidwell and Holland 2002). Other work has considered whether diversity is actually just a reflection of rock outcrop availability (e.g. Raup 1972, 1976; Peters and Foote 2001, 2002; Smith 2001, 2007; Smith *et al.* 2001; Crampton *et al*. 2003; Foote 2003; Peters 2005; Smith and McGowan 2005, 2007).

Taphonomy became an established branch of vertebrate palaeontology in the 1960s-70s, largely through the work of Olson (1962), Voorhies (1969), Dodson (1971) and Behrensmeyer (1975). Although taphonomic principles had been used in dinosaur studies (Hennig 1925; Weigelt 1927; Gilmore 1932) to some extent long before Efremov (1940) named this field of palaeontology, it wasn't until the 1946-1949 Mongolian Paleontological Expedition that taphonomic studies of dinosaurs began in earnest (Efremov 1954).

Taphonomy has also been combined with spatial and temporal distributions of specimens to assess palaeoecological aspects of dinosaurs (Béland and Russell 1978; Dodson *et al*. 1980a, b; Winkler and Rose 2006). Additionally, taphonomic studies of exceptionally preserved dinosaur specimens or assemblages have enabled numerous palaeobiological hypotheses to be tested, such as gregarious behaviour and parental care (e.g. Horner and Makela 1979; Norman 1987; Zhao *et al*. 2007; see also Weishampel *et al*. 2004b, and references therein). Based on various taphonomic criteria, Behrensmeyer *et al*. (1979) predicted that large animals may be overrepresented in the fossil record; conversely, however, the likelihood of large

animals being completely preserved is greatly reduced given the larger amount of sediment needed for rapid burial. As a result, complete sauropod skeletons are extremely rare occurrences and very few complete or partial skulls are known (Upchurch *et al*. 2004a). The following studies have been selected from the vast taphonomy literature as these represent a variety of different approaches to the analysis of taphonomic patterns and are particularly applicable to the problem of studying large palaeo-vertebrates.

Disarticulation Patterns

The disarticulation pattern of vertebrates has been the subject of a number of papers (e.g. Weigelt 1927; Müller 1950; Schäfer 1962, 1972; Toots 1965; Dodson 1971, 1973; Bourn and Coe 1979; Hill 1979; Smith 1980, 1993; Bickart 1984; Hill and Behrensmeyer 1984; Meyer 1991; Sander 1992; Oliver and Graham 1994; Dodd 1995; Davis and Briggs 1998; Hungerbühler 1998; Heinrich 1999; Bandyopadhyay *et al*. 2002; Brand *et al*. 2003a, b; Ray and Bandyopadhyay 2003). Hill (1979) described a statistical technique for determining the disarticulation sequence of a mammal and applied it to a bone assemblage of the modern antelope *Damaliscus korrigum* from East Africa. Hill (1979) considered this an important issue based on several factors:

1. Ecological and environmental conditions are reflected in variations in disarticulation sequences.
2. The ends of bones are exposed by the process of disarticulation, leading to weathering, fracturing, abrasion, etc.
3. Disarticulation reduces a skeleton into a number of small parts, making transport and thus scattering much easier. This may also have an effect on the relative proportions of certain body parts within bone accumulations.
4. The amount of disarticulation can provide an estimate of the length of the interval between death and burial.

Hill (1979) noted that the main problems with most previous analyses of disarticulation were the use of either a single carcass studied over a period of time or the study of a number of carcasses at different stages of disarticulation. In both cases there is a difficulty in quantitatively assessing the disarticulation process. To overcome this issue, he analysed the relative numbers of different intact joints in the whole assemblage of antelopes. This number is a function of the number of that particular joint in a single skeleton and the length of time that joint remains intact posthumously. To eradicate this problem, Hill (1979) divided each frequency by the number of that joint within the whole skeleton; this left him with a value indicating the relative longevity of the joints and thus reflecting the disarticulation sequence (Figures 1.17 and 1.18).

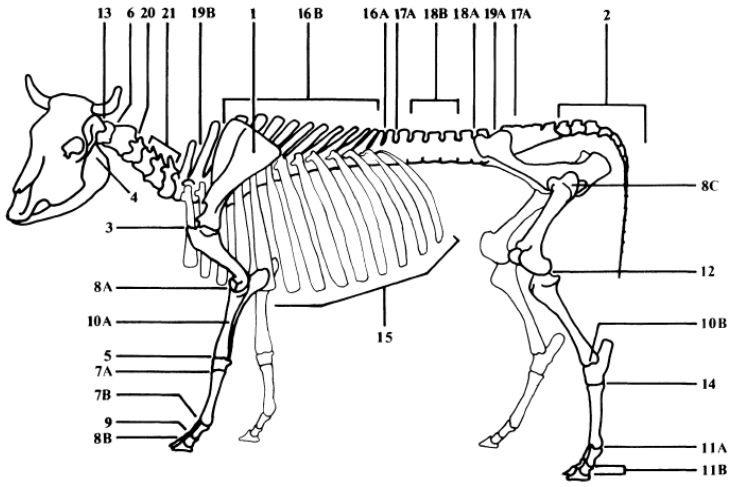

FIGURE 1.17. The order of disarticulation in *Damaliscus korrigum* (illustrated using a drawing of a cow skeleton). Numbers indicate the order in which different bones separate (after Hill 1979).

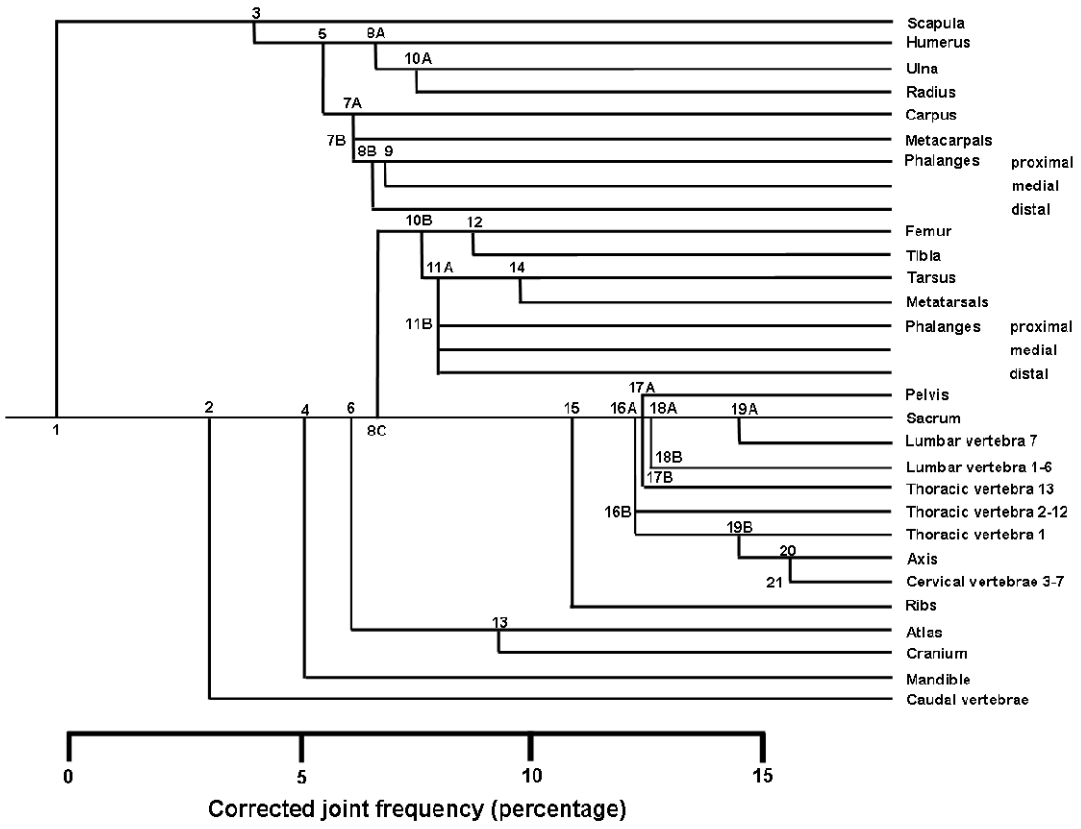

FIGURE 1.18. Statistical scheme of disarticulation in an ideal skeleton of *Damaliscus korrigum* (see Fig. 1.17). The left of the diagram represents a complete skeleton which disarticulates into single bones across to the right. The y-axis gives the corrected frequency of joints, which reflects their durability and relative times of disarticulation (after Hill 1979).

Hill and Behrensmeyer (1984) used this technique to determine the disarticulation patterns of a wide range of African mammals in a tropical savannah environment. Their work showed that, although there is some variation among species, overall the process is very consistent. Behrensmeyer (1978) established a relationship between bone weathering and years since death and this was used to calibrate the timescale of disarticulation, which showed that most disarticulation is complete approximately five years after death (see following section). A few species demonstrated slight variation to

this timescale; for example, the cervical vertebrae of buffalo were still articulated 6.5 years after death and some smaller species seemed to disarticulate slightly more rapidly than larger ones (Hill 1980; Hill and Behrensmeyer 1984). The authors concluded that disarticulation in a single environment is very consistent, even for mammals of different taxa and size (although they highlighted that this may be related to their overall similarity in *bauplan*). Hill and Behrensmeyer (1984) also noted that different environments may produce different disarticulation sequences and that other animals may have an effect on disarticulation (i.e. by scavenging and trampling). It has been suggested that arid and aqueous environments show characteristic sequences of limb disarticulation: in dry terrestrial conditions, limb disarticulation tends to begin proximally and proceed distally, while the opposite trend occurs in aqueous environments (Hill 1979; Brand *et al.* 2003a).

Both Hill (1979) and Hill and Behrensmeyer (1984) indicated the importance and potential use of understanding the processes of disarticulation in palaeontological investigations and its particular relevance to processes of transportation. Likewise, disarticulation can also provide an estimate of the time interval between the death of an organism and its subsequent burial. Fossils with articulated elements that should disarticulate early are indicative of fairly rapid burial; isolated elements from areas of the skeleton expected to remain articulated until late in the disarticulation process indicate that there was a significant time interval between death and burial. This also helps to predict associated occurrences, as those elements remaining articulated longest would be expected to be found together even after disarticulation, in comparison to bones that disarticulate early (Hill and Behrensmeyer 1984).

Smith (1980, 1993) investigated the taphonomy of therapsids in the Late Permian Karoo Basin of South Africa. Based on field observations of approximately 2500 *in situ* fossils he identified regularly occurring patterns of skeletal disarticulation that he grouped into eight taphonomic classes (Table 1.1).

TABLE 1.1. Taphonomic classes of *Diictodon* based on the degree of disarticulation of the skeleton (after Smith 1993).

Description	Class	Taphonomic class	Transportation	Preburial period
Preserved at site of death	A	Complete articulated skeleton in "curled up" attitude	No transportation	Very short
Preserved at site of death	B	Complete or near complete skeleton with straight spinal curvature	Slightly rolled	Short
Preserved near site of death	C	Skull with articulating cervicals and mandibles	Slightly rolled	Short
Preserved near site of death	D	Skull with displaced mandibles	Short distance transportation	Long
Preserved near site of death	E	Skull without mandibles	Short distance transportation	Long
Preserved near site of death	F	Mandibles	Short distance transportation	Long
Preserved far from site of death	G	Accumulation of small postcranial elements into bonebed	Long distance transportation; winnowed and sorted	Very long
Preserved far from site of death	H	Isolated and/or fragmented postcranial elements	Long distance transportation	Very long

The absence of animals with dentition capable of crushing long bones led Smith (1993) to suggest that carnivory was not a major factor in disarticulation in the Late Permian Karoo Basin; instead he hypothesised that the range in degree of disarticulation reflected differing periods of exposure before burial. The author demonstrated that the preservation potential of certain regions of the floodplain was considerably higher than the rest (reflecting higher sedimentation rates) for extended periods of time, resulting in clusters of fossils preserved in the successive alluvial layers.

Isolated skulls were demonstrated to be the dominant taphonomic class amongst the Karoo fossils (Fig. 1.19). *Diictodon* is the most common Late Permian genus in the Karoo Basin. Their skulls are the largest and heaviest single element of the skeleton (especially when the lower jaw remains articulated, as is the case in the majority of isolated skulls in the Karoo Basin). This means that of all the disarticulated elements the skull was the least likely to have been transported (Smith 1993).

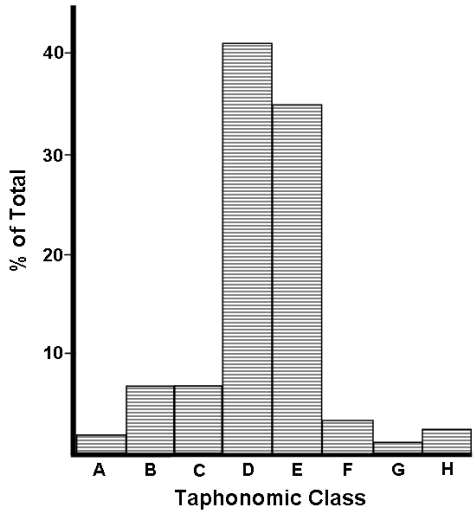

FIGURE 1.19. Relative abundance of taphonomic classes amongst all fossils found in the Karoo study sections (after Smith 1993). Note the dominance of isolated skulls and the overall paucity of individual postcranial elements. See Table 1.1 for taphonomic classes.

Dodson (1971) studied the sedimentology and taphonomy of the dinosaur-rich, Campanian (Late Cretaceous) Oldman Formation in Alberta, Canada. He noted that the dinosaurs demonstrated a wide spectrum of degrees of articulation and assigned the specimens to a range of taphonomic classes (Table 1.2).

TABLE 1.2. Taphonomic scheme illustrating the degree of disarticulation of dinosaur specimens from the Campanian (Late Cretaceous) Oldman Formation in Alberta, Canada (after Dodson 1971).

Class	Condition
A	Specimen complete or nearly so
B	Specimen complete or nearly so; some drifting of major elements
C	Skull and scattered skeleton
D	Skull and scattered bones
E	Skeletons without heads
F	Skull with incomplete articulated skeleton
G	Incomplete articulated skeleton
H	Skull with jaws
I	Skull without jaws
J	Isolated bones
K	Incomplete articulated specimens (extent of original specimen unknown)

Class A specimens were interpreted as having been buried rapidly after death, with many of these found in channel environments, suggesting the animals lived very close to the water and perhaps died in the water (Dodson 1971). Headless skeletons (E) and drifted skeletons (B) represent early stages of disarticulation in channel settings and quiescent water environments respectively. As can be seen from Figure 1.20, there is a large spectrum of resultant specimens at different stages and combinations of disarticulation (Dodson 1971).

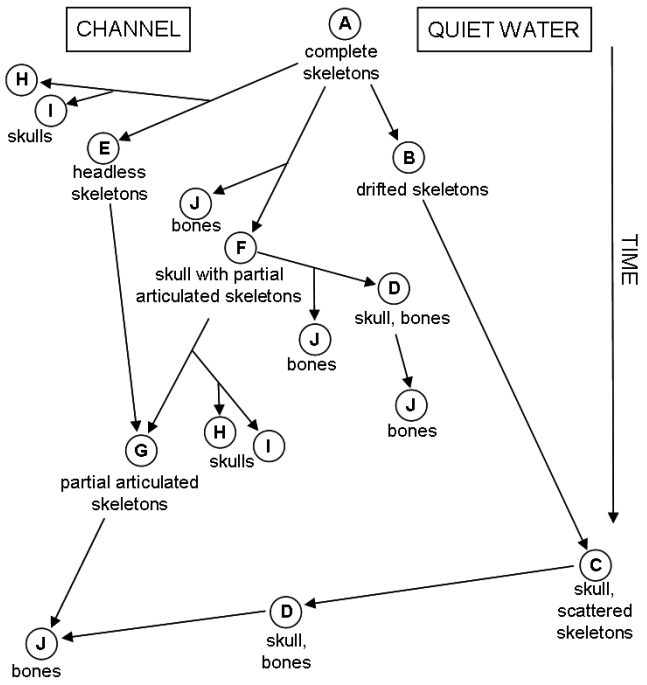

FIGURE 1.20. Interrelationships of the various stages of decomposition. See Table 1.2 for description of taphonomic classes (after Dodson 1971).

Plateosaurus is one of the most common dinosaurs, with well over 100 specimens preserved (Galton and Upchurch 2004). Weishampel (1984) and Sander (1992) investigated the taphonomy of this dinosaur, and both workers organised the specimens into completeness groupings (Table 1.3), similar to that of Dodson (1971).

Sander (1992) noted that complete skeletons show the animal lying on its stomach (the posterior end of the dorsal series) with the anterior end twisted and lying on its side. The neck tends to curve towards the neural spine (in an opisthotonic posture), with the anterior cervical vertebrae pointing in a different direction to the skull (which tends to be on its side). Sander (1992) also identified the main area of weakness in the skull as being at the nasal-frontal suture, and this is the point from which disarticulation tends to begin. The posterior portion of the skull disassociates from the anterior part (which includes the mandibles); the elements of the posterior part then progressively

disarticulate while the anterior elements and mandibles tend to remain attached. The pelvis was shown to usually be found in an upright position with the tail recurved over the back. Scapulocoracoids tended to be found in life position, while the forelimbs were usually spread away from the body in a horizontal position, with the humerus commonly in articulation with the scapulocoracoid. The femur tended to be pulled forward about 45° and Sander (1992) noted a strong bend in the knee so that the lower leg points backwards. The bones were actually sloping down into the sediment, resulting in the pedes being very deep within the sediment.

TABLE 1.3. Completeness classes of *Plateosaurus* specimens (after Sander 1992).

Body region	Class	Elements lost	Disarticulation
Skeleton	A	None	None
Skeleton	B	Few	Little
Skeleton	C	Few	Some
Skeleton	D	Many	Strong
Posterior half	E	None	None
Posterior half	F	Few	Some
Posterior half	G	Many	Considerable
Anterior half	H	None	None
Anterior half	I	Few	Some
Anterior half	J	Many	Considerable
Bones	K	Fields	Considerable
Bones	L	Isolated finds	Considerable

Some *Plateosaurus* skeletons are complete and intact but, in many cases, only the posterior half of the skeleton is preserved (in various stages of completeness and disarticulation). Very few specimens preserve anterior body regions and these patterns are extremely similar for all four *Plateosaurus* bonebeds (Figures 1.21 and 1.22). Sander

(1992) suggested that a miring event would best account for the type of preservation seen, with individuals becoming mired in mudholes on a semiarid floodplain. He postulated that the typical poses seen in the skeletons were the result of their struggle to free themselves. The processes of weathering and scavenging (indicated by the presence of theropod teeth in the deposits) removed elements not embedded in the mud; however, in many instances the carcass was left to mummify, resulting in the characteristic pattern of the strongly recurved neck and tail displayed by most complete skeletons (Sander 1992; though see Faux and Padian [2007] for an alternative explanation of opisthotony in vertebrate skeletons).

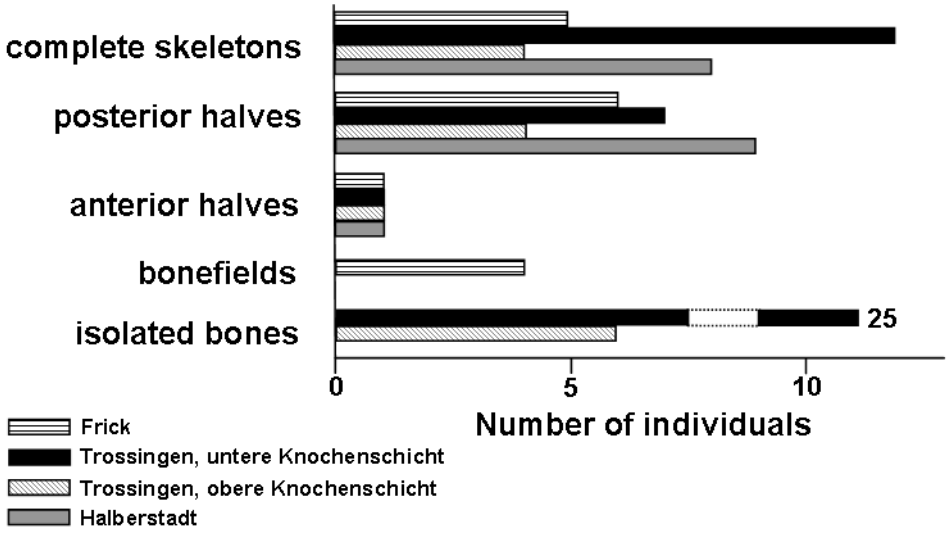

FIGURE 1.21. Frequency of the different body regions in four *Plateosaurus* samples. In general, there is an overwhelming predominance of complete skeletons and posterior halves (after Sander 1992).

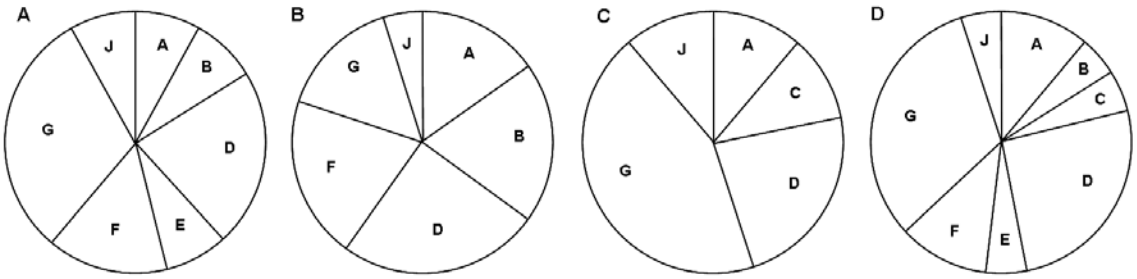

FIGURE 1.22. Comparison of relative frequencies of completeness classes and body regions of *Plateosaurus*. Note the distinct similarity of all four samples. (A) Frick (no. of individuals [n] = 13), (B) Trossingen untere Knochenschicht (n = 20), (C) Trossingen obere Knochenschicht (n = 9), and (D) Halberstadt (n= 19). See Table 1.3 for description of classes and body regions (after Sander 1992).

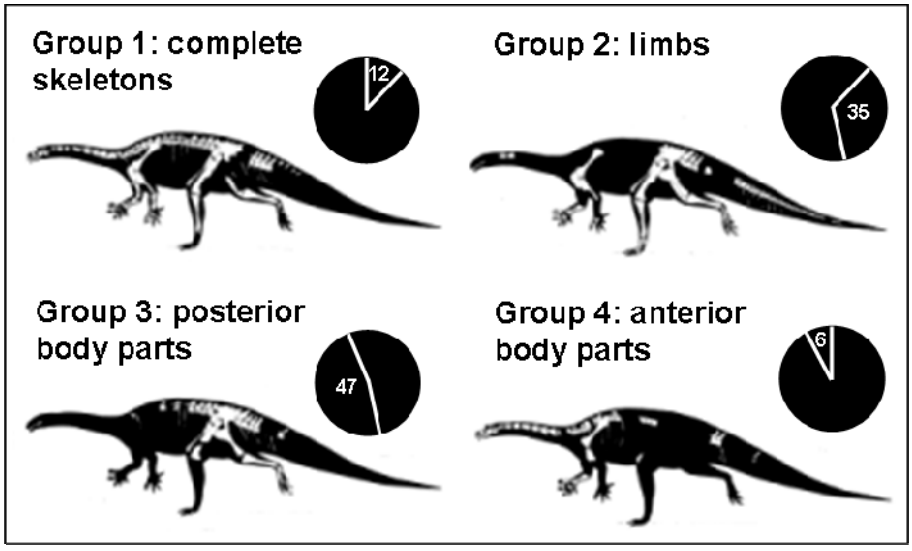

FIGURE 1.23. Skeletons of '*Sellosaurus*' *gracilis* from the lower and middle Stubensandstein, showing completeness groups and percentual distribution (after Hungerbühler 1998).

Hungerbühler (1998) carried out a similar analysis for the prosauropod '*Sellosaurus*' *gracilis* (now separated into *Efraasia minor* and *Plateosaurus gracilis*; Yates [2003b]),

grouping the material into four different completeness groups (Fig. 1.23). Hungerbühler (1998) noted that, like the *Plateosaurus* specimens that Sander (1992) studied, this was a mono-taxic site (though the more recent work of Yates [2003b] suggests that at least two taxa were present) and that there is a predominance of posterior skeletal parts; also the skeletons are preserved 'belly down'. The preservational states and burial postures of the specimens led Hungerbühler (1998) to propose that they reflected *in situ* preservation of individuals, most likely by miring in unconsolidated fluvial sands covered by floodplain deposits. Shed teeth of carnivores also led the author to suggest that some of the carcasses were scavenged.

TABLE 1.4. Disarticulation stages of Tendaguru dinosaur skeletons (after Heinrich 1999).

Disarticulation stages	**Designation**	**Skeletal elements**
A	Complete skeleton	Articulated; no loss of bones
B	Complete skeleton	Partly articulated; no loss of bones
C	Complete skeleton	Disarticulated; no loss of bones
D	Incomplete skeleton	Articulated; loss of bones
E	Incomplete skeleton	Partly articulated; loss of bones
F	Incomplete skeleton	Disarticulated; loss of bones
G	Complete partial skeleton	Articulated; no loss of bones
H	Complete partial skeleton	Partly articulated; no loss of bones
I	Complete partial skeleton	Disarticulated; no loss of bones
K	Incomplete partial skeleton	Articulated; loss of bones
L	Incomplete partial skeleton	Partly articulated; loss of bones
M	Incomplete partial skeleton	Disarticulated; loss of bones
N	Bone field	Partly associated
O	Bone field	Disassociated
P	Isolated bone	Isolated

Heinrich (1999) studied the taphonomy of the dinosaurs from the Late Jurassic of Tendaguru, Tanzania. He used a similar measure of completeness as previous authors (Dodson 1971; Sander 1992; Smith 1993; see above), as shown in Table 1.4. Heinrich (1999) noted that stages of disarticulation ranged from incomplete skeletons to isolated bones and he argued that the evidence suggested that there was carcass decay and post-mortem transport before burial, also indicated by a certain amount of abrasion present on the remains. The occurrence of bones in several superimposed horizons led Heinrich (1999) to postulate that the remains accumulated over a long time span.

Davis and Briggs (1998) implemented taphonomic experiments on modern bird carcasses in brackish and marine environments. To test for the effect of scavengers on the bird carcasses, the authors placed some specimens in cages and left some exposed; both showed similar sequences of decay:

1. The carcass remained essentially intact for up to three days.
2. The skeleton remained complete but the soft tissues decayed and loosely attached feathers began to detach.
3. The skeleton disarticulated in (generally) the following order:

(a) Skull and cervicals disarticulated from the thoracic region, with the skull also usually separating.
(b) Femur separated from the synsacrum.
(c) Pectoral girdle detached from the thoracic region though remained articulated with the forelimbs.
(d) Posterior thoracic vertebrae began to disarticulate resulting in the separation from the synsacrum.
(e) Thoracic ribs separated from thoracic vertebrae, which, in turn, disarticulated into separate vertebrae.
(f) Limbs disarticulated.

(g) Pectoral girdle elements disarticulated.

4. Elements remained associated, though some smaller bones were often removed by currents.
5. Only isolated, completely disarticulated skeletal elements remained.

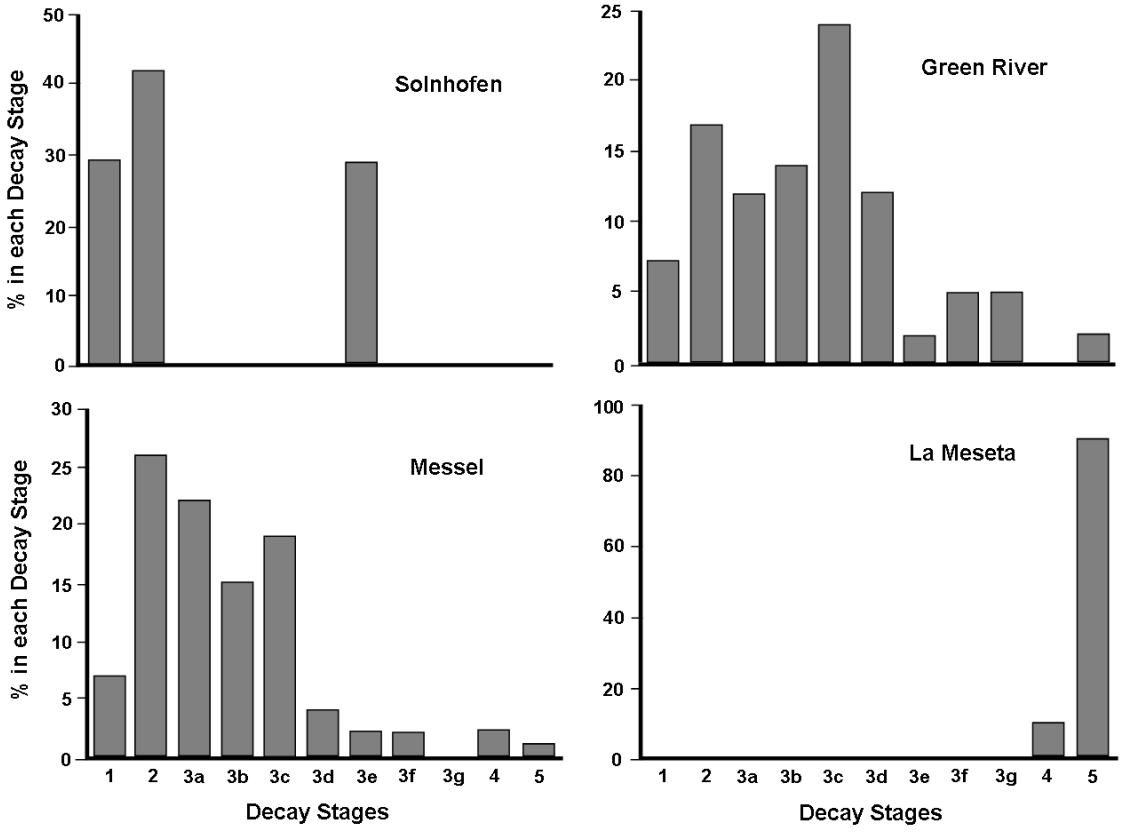

FIGURE 1.24. Proportion of bird specimens (expressed as a percentage of the total) in each decay stage in four selected Fossil- Lagerstätten showing the gradation in completeness from the Solnhofen Limestone, via Messel and the Green River Formation (Fossil Lake) to the La Meseta Formation. See text for explanation of decay stages (after Davis and Briggs 1998).

With the addition of scavenging, the process of disarticulation was shown to occur much more rapidly, with some of these stages not being observed (Davis and Briggs 1998). The

authors then used this to study the disarticulation sequences of four contrasting bird fossil lagerstätten, allocating each specimen to a decay stage. The authors noted that total disarticulation is usually the most common preservational state for fossils. They also commented that the distribution of carcasses among the different disarticulation stages emphasizes the contrasts between the taphonomic histories of birds from the four different localities (Fig. 1.24). The hypersaline conditions and anoxia that prevailed in the Solnhofen Sea and at Messel, respectively, inhibited scavengers. Rapid burial also reduces the possibility of scavenging and they postulated that this may have been a factor in both the Solnhofen and the Green River Formation. However, the La Meseta Formation is characterized by wave- and tide-dominated sedimentation; thus, transport accounts for the disarticulation of the skeletons at this locality (Davis and Briggs 1998).

Brand *et al*. (2003a) conducted a study to examine the timing and nature of decay and disarticulation in a range of small modern vertebrates. These were studied in both freshwater and seawater settings as well as in a terrestrial environment (which was protected from scavengers by cages). In both water settings, carcasses varied in the amount of time they floated before sinking occurred. For example, amphibians floated only for a few days while mammals often sank relatively quickly before then floating for a month or more. Birds, however, did not sink until they were completely falling apart. In water, the flesh decayed due to bacterial action within six months, while on land this happened within two weeks due to the hatching of insect larvae. Differences in skin properties also had an affect on the decay process: the dry skin of birds, mammals and salamanders, for example, changed very little for up to eleven months. Brand *et al*. (2003a) demonstrated that disarticulation time was shortest in water and longest in a dry terrestrial environment for all species. In terrestrial conditions disarticulation time was shown to also increase with carcass size for birds, mammals and salamanders, but size had no effect in either water environment. The beginning of the rainy season had a significant effect on the disarticulation time in terrestrial conditions, with disarticulation greatly accelerating as a result. The disarticulation sequence tended to vary

considerably, particularly within the terrestrial environment, but skulls and limbs were generally the first to separate from the body, followed by further disarticulation of the elements comprising the limbs. There was wide variability in the disarticulation time of vertebrae, with some coming loose very early in the disarticulation process and others remaining in articulation well into the process. The authors noted a similar variability in the disarticulation of the manus and pes. Salamander skulls tended to disarticulate very quickly, while lizard skulls were more durable but eventually fell apart. Mammal and bird skulls, although separating early from the body, were shown to be fairly resistant to further disarticulation. Brand *et al*. (2003a) highlighted the fact that these data could be used as an analogue for fossil assemblages, providing upper limits for interpretations of time from death to burial. For example, an assemblage containing partially or fully articulated small vertebrates was likely to have been buried within a few months or years after death in water and on land, respectively. The authors (p. 92) noted a few areas were the need to err on the side of caution was required: for example, the tendency of amphibian and reptile skin to 'hold together as a strong but limp bag with bones inside' could lead to some articulated fossils being misinterpreted as products of rapid burial.

Weathering patterns

Behrensmeyer (1978) proposed a scheme (Table 1.5) for describing the weathering characteristics of the bones of recent mammals. She noted that the bones of mammals from Amboseli Park, in southern Kenya, exhibited distinctive weathering characteristics which were related to the time since death, as well as to temperature, humidity and soil chemistry conditions.

Behrensmeyer (1978) also looked at the rate of weathering, and demonstrated that there was a general relationship between the degree of weathering and the amount of time since death (Table 1.6). Although there was considerable variation between stages

3-5, she noted that no carcass older than three years showed weathering stages of 0-1: the degree of weathering was always much more substantial by this point. She also noticed that there was no consistent association between habitat and weathering stage, and that localised conditions (e.g. vegetation, moisture and shade) were much more significant in determining the degree of weathering.

TABLE 1.5. Bone weathering categories based on mammal carcasses from Amboseli Park, Kenya (after Behrensmeyer 1978).

Stage	Description
0	Bone surface shows no sign of cracking or flaking; bone still greasy; tissue still present in inner cavity; flesh still attached to bone in places
1	Bone shows cracking, normally parallel to bone fibre; mosaic cracking of covering tissue and bone at joints; flesh may or may not still be attached
2	Flaking of surface layers of bone; deeper and more extensive flaking follows until most of the outer bone is gone
3	Patches of homogeneously weathered compact bone characterised by a fibrous texture; gradually becomes more extensive
4	All bone surfaces are coarsely fibrous and rough in texture; weathering beginning to penetrate inner cavities
5	Bone is falling apart in situ; cancellous bone exposed; original shape of bone difficult to determine

Behrensmeyer (1978) also highlighted the potential use of such a scheme for the study of fossil vertebrates and Fiorillo (1988) modified her weathering stages for just such a purpose. He modified her scheme to take into account the fact that fossil bones never have any grease or flesh on them, reducing it to four stages (Table 1.7).

TABLE 1.6. Weathering stages related to number of years after death of the carcass in Amboseli Park, Kenya (after Behrensmeyer 1978).

Stage	Range in years since death
0	0-1
1	0-3
2	2-6
3	4-15 +
4	6-15 +
5	6-15 +

TABLE 1.7. Bone weathering categories for fossil bones from Hazard Homestead Quarry, Hitchcock County, Nebraska (after Fiorillo 1988).

Stage	Description
0	No sign of cracking or flaking of surface layers of bones
1	Bone shows cracking, parallel to bone fibres; some mosaic cracking
2	Flaking of surface layers of bone; cracking beginning to penetrate inner cavities
3	Outermost bone gone; surface has fibrous texture and most cracks penetrating inner cavities

These weathering classifications, or slight modifications of them, have been used in countless subsequent studies of vertebrates (e.g. Dodson 1980a, b; Hill and Behrensmeyer 1984; Wood *et al*. 1988; Cook 1995; White *et al*. 1998; Pereda-Suberbiola *et al*. 2000; Ryan *et al*. 2001; Bandyopadhyay *et al*. 2002; Brand *et al*. 2003b; González Riga and Astini 2007; Myers and Storrs 2007; Suarez *et al*. 2007).

Bone abrasion patterns

Based partly on the work of Hunt (1978), Fiorillo (1988) presented a scheme for defining the degree of abrasion of fossil bones. In doing this he incorporated the terminology used in sedimentology for describing the roundness of grains and proposed a four-stage classification (Table 1.8).

TABLE 1.8. Bone abrasion categories for fossil bones from Hazard Homestead Quarry, Hitchcock County, Nebraska (after Fiorillo 1988).

Stage	Description
0	no abrasion – edges and processes still sharp and well-defined
1	slight abrasion – some rounding of the edges and processes
2	moderate abrasion – edges well rounded; processes reduced to protrusions on bone
3	high abrasion – edges extremely well rounded; processes abraded away; reduced to bone pebble in extreme cases

In a similar way to the weathering schemes proposed by Behrensmeyer (1978) and Fiorillo (1988), the abrasion classification (or slight modifications of it) of Fiorillo (1988) has also been used in numerous subsequent taphonomic studies (e.g. Cook 1995; Pereda-Suberbiola *et al*. 2000; Ryan *et al*. 2001; González Riga and Astini 2007; Suarez *et al*. 2007).

Discussion

Disarticulation patterns are relatively well known for many modern vertebrates (e.g. birds, African mammals, lizards; Hill 1979; Hill and Behrensmeyer 1984; Davis and Briggs 1998; Brand *et al*. 2003a), but only one study has been implemented that compares these patterns with extinct groups (i.e. Davis and Briggs 1998). A number of studies of

extinct animals have looked at which body regions tend to be preserved (e.g. Sander 1992; Smith 1993; Heinrich 1999), but these have all been limited to the study of a single assemblage or geographical region.

Although weathering and abrasion schemes are extremely useful in determining the taphonomic history of an animal when studying recently excavated material, both are very difficult to utilise for specimens that have been stored in museums for decades or possibly even over a century. This is because specimens become abraded and broken through examination and movement, meaning that distinguishing genuine taphonomic marks from more recent damage is extremely problematic. In addition, most descriptive papers provide little or no taphonomic information, making collection of a large amount of data unfeasible. As such, neither an abrasion nor weathering classification is suitable for a large-scale study of sauropodomorph taphonomy.

There is scope for large-scale analyses looking at the disarticulation patterns of sauropodomorphs, as this has never been implemented in any great detail for extinct animals, with previous analyses restricted to bonebed assemblages. A study considering which body regions tend to be most commonly preserved for all sauropodomorph individuals would also be the first to be applied at such a large-scale (previous studies have all been of mono-taxic assemblages or single geographic regions [see above]).

CHAPTER TWO

MATERIALS AND METHODS

DATA

Biological data

A global relational database of all known sauropodomorph occurrences (body fossils and tracksites) has been constructed (using Microsoft Access), including detailed information on geographic location, geological setting, palaeoenvironmental indicators, stratigraphic age, taphonomy and taxonomic composition. These data were gathered from the primary literature, *The Paleobiology Database* (www.paleodb.org; Carrano 2008b) and personal observations of specimens in museum collections (Table 2.1); the latter has enabled the addition of undescribed specimens into the database as well as facilitating identification of the phylogenetic affinities of numerous specimens (e.g. recognition of a UK rebbachisaurid and a Chinese diplodocid from museum visits; Mannion 2009a; Upchurch and Mannion 2009). The resultant database consists of 2322 occurrences (2024 body fossils and 298 tracksites). This consists of almost entirely museum catalogued specimens, with most described in the literature. Field notebooks were not studied but published information on specimens left in the field has been incorporated (although such occurrences were rare). This admittedly means that some specimens may only represent a subset of what was actually preserved. Different analyses use various subsets of this dataset and are outlined below. Comparable data on all named ornithischians (720 body fossils and 208 tracksites) have been extracted from *The Paleobiology Database*, while the ornithischian element (composed of body fossils and tracksites) of the Cretaceous dataset of Butler and Barrett (2008) has been used to further supplement comparisons between the two herbivorous dinosaur clades. These comparisons are important not only to see where the two herbivorous groups co-existed but also (and possibly more usefully) where they did not co-exist. Ornithischians, rather than theropods, are used for this comparison with sauropodomorphs for two reasons: first, as herbivores they may have required the same food groups as sauropodomorphs and thus potentially lived in the same regions (although naturally it is

to be expected that many theropods would also have lived in the same environments as their prey). Second, the Cretaceous dataset of Butler and Barrett (2008) is limited to herbivorous dinosaurs, which therefore excludes most theropods. Sauropodomorph taxic diversity has been extracted from this database, with 175 taxa considered valid as of September 2008 (see 'Taxonomic Revision' below). Ornithischian diversity has also been compiled from this dataset (Carrano 2008b; www.pbdb.org). The sauropodomorph phylogenies of Wilson (2002), Upchurch *et al*. (2004a, 2007a), Yates (2007) and Lloyd *et al*. (2008) have all been utilised. All data not listed in the text are supplied in the Supplementary Appendix.

TABLE 2.1. List of museums and repositories visited for study of sauropodomorph material.

Country	Museums/repositories
China	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
China	Long Hao Geologic and Paleontological Research Center, Hohhot, Inner Mongolia
Germany	Dinosaurier Freilichtmuseum, Münchehagen
Germany	Museum für Naturkunde, Berlin
Sweden	Paleontological Museum, Uppsala
S. Africa	Bernard Price Institute for Palaeontological Research, Johannesburg
S. Africa	South African Museum (Iziko Museums of Cape Town), Cape Town
UK	Dinosaur Isle Visitor Centre, Isle of Wight
UK	Natural History Museum, London
USA	American Museum of Natural History, New York
USA	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
USA	Cleveland Museum of Natural History, Ohio
USA	Denver Museum of Nature and Science, Denver, Colorado
USA	Field Museum of Natural History, Chicago, Illinois
USA	Glenrock Paleontology Museum, Glenrock, Wyoming

USA	Peabody Museum of Natural History, Yale University, New Haven
USA	Rocky Mountain Dinosaur Resource Center, Woodland Park, Colorado
USA	Smithsonian National Museum of Natural History, Washington D.C.
USA	University of Chicago, Illinois
USA	University of Wyoming Geological Museum, Laramie, Wyoming
USA	Wyoming Dinosaur Center, Thermopolis, Wyoming

Sampling data

Data have been collected from *The Paleobiology Database* on all Mesozoic dinosaur-bearing collections (DBCs), including avian dinosaurs; the resultant dataset consists of 5454 collections. Information on the number of dinosaur-bearing formations has been extracted from Upchurch and Barrett (2005), while data on the amount of terrestrial and marine rock outcrop in western Europe has been gathered from Smith and McGowan (2007). Lastly, data on Mesozoic and Late Cretaceous sea levels have been collected from Haq *et al*. (1987) and Miller *et al*. (2005), respectively.

GEOGRAPHICAL INFORMATION SYSTEMS (GIS)

GIS is a computer-based system used to input, store, retrieve, manipulate, analyse and output geographically referenced data or geospatial data. GIS is a tool that allows users to create interactive queries, analyse the spatial information, edit data and maps, and present the results of all these operations. It functions as a series of digital maps in which different data sets are stored as independent layers (Theobald 2003). GIS plays an important role in helping support decision making for planning and management of land use, natural resources, environment, transportation, urban facilities, and other administrative records. There are also advantages of GIS over a standard database in that it enables inventorying, updating, querying and analysis of spatial relationships across numerous layers of mapped information (Rayfield *et al*. 2005).

However, GIS need not only be used to analyse spatial relationships and patterns; there is also the potential to incorporate a temporal aspect into analyses (Berry 1995; Chou 1997; Burrough and McDonnell 1998; Rayfield *et al*. 2005; Stigall Rode 2005). This can be implemented using palaeogeographic maps and through conversion of modern day co-ordinates into palaeolatitudes and palaeolongitudes. In recent years there has been a growing use of GIS in palaeontological studies as workers have realised its use in enabling the testing of palaeobiological hypotheses. The primary use of GIS in many of these analyses has been to create geospatial databases of fossil localities (e.g. Benton *et al*. 2001; Ferguson *et al*. 2001; Lacruz *et al*. 2003; McKinney *et al*. 2003, 2004; Nigro *et al*. 2003; Jennings and Hasiotis 2006). However, several analyses have looked at a range of problems, including: the responses to groups of animals to environmental fluctuations (Graham *et al*. 1996; Barnosky and Carrasco 2000; Markwick 2002; Davis 2005a), palaeobiogeographical issues (Rode and Lieberman 2004, 2005; Sanchez-Cordero *et al*. 2004; Stigall Rode 2005; Stigall Rode and Lieberman 2005; Stigall and Lieberman 2006; Holmes 2007), biochronology (Rayfield *et al*. 2005), palaeodiversity studies (Davis 2005b; Vermeesch 2005; Butler *et al*. 2009a, b), fossil site prediction

(Mensing *et al*. 2000; Oheim 2007) and the testing of co-evolutionary scenarios (Butler *et al*. 2009a, b). GIS has also been used in several morphological studies (e.g. Jernvall *et al*. 2000; Ungar and Williamson 2000; M'Kirera and Ungar 2003; Yacobucci and Manship 2003; Manship 2004).

GIS has been utilised primarily as a visual tool in this study. All co-ordinate data have been converted into palaeolatitudes using the PointTracker software of Scotese (2004). Data have been exported into ArcGIS 9.2, within which different queries can be run, allowing the creation of spatial layers for individual timeslices and thereby incorporating a temporal element into the usage of GIS. Distributions of sauropodomorph occurrences have been plotted on palaeocontinental reconstructions (using the software of Scotese [2001]).

TAXONOMIC REVISION

Except where stated, sauropod taxonomy follows that of Upchurch *et al*. (2004a) in terms of phylogenetic position and validity of taxa. Basal sauropodomorph and prosauropod taxonomy is largely based on the analyses of Upchurch *et al*. (2007a) and Yates (2007). Below is a discussion of taxa considered to be in a phylogenetic position different to that postulated by Upchurch *et al*. (2004a) and these considerations are based both on more recent literature and also from personal observations. Table 2.2 lists all taxa (175) considered valid (including generically distinct, but unnamed, taxa), including their stratigraphic ranges. The latter is discussed in detail later in this chapter ('Diversity: Taxic and phylogenetic diversity estimates: Geological ages of taxa').

TABLE 2.2. List of all sauropodomorph taxa considered valid in this study (as of September 2008). References are provided for taxa that have either been named since Upchurch *et al*. (2004a) or whose phylogenetic position or validity has since been modified (see also text). The stratigraphic range for each taxon is also provided. Abbreviations: E = Early; M = Middle; L = Late. Note that these analyses included *Jobaria* as an Early Cretaceous taxon, whereas Rauhut and López–Arbarello (2009) have since argued for a Middle Jurassic age. Additionally, *Tehuelchesaurus* was erroneously included as a late Middle Jurassic taxon, following Rich *et al*. (1999; see also Upchurch *et al*. 2004a; Weishampel *et al*. 2004a), whereas Rauhut *et al*. (2005) showed that it is Late Jurassic.

Taxon	Earliest stage	Latest stage	Taxonomic position	Reference
"*Apatosaurus minimus*"	Kimmeridgian	Tithonian	Macronaria	—
"*Cetiosauriscus greppini*"	E. Kimmeridgian	E. Kimmeridgian	Eusauropoda	Schwarz *et al*. 2007
"*Cetiosaurus glymptonensis*"	L. Bathonian	L. Bathonian	Diplodocoidea	—
"*Cetiosaurus*	Kimmeridgian	Kimmeridgian	Brachiosauridae	—

humerocristatus"				
"Cloverly titanosaur"	Aptian	Aptian	Titanosauria	pers. obs. 2008
"*Gyposaurus sinensis*"	Hettangian	Sinemurian	Prosauropoda	Upchurch *et al*. 2007a
"*Huanghetitan ruyangensis*"	Cenomanian	Santonian	Titanosauriformes	Lü *et al*. 2007b
"McCoy Brook prosauropod"	Hettangian	Hettangian	Prosauropoda	Fedak 2006
"*Morosaurus agilis*"	Kimmeridgian	Tithonian	Sauropoda	—
"*Yunnanosaurus youngi*"	Aalenian	Callovian	Prosauropoda	Lü *et al*. 2007a
Abrosaurus	Bathonian	Callovian	Macronaria	—
Adamantisaurus	Campanian	Maastrichtian	Lithostrotia	Santucci & Bertini 2006
Aegyptosaurus	E. Cenomanian	E. Cenomanian	Titanosauria	—
Aeolosaurus	L. Campanian	E. Maastrichtian	Lithostrotia	—
Agustinia	Aptian	Albian	Titanosauria	—
Alamosaurus	L. Campanian	Maastrichtian	Lithostrotia	—
Amargasaurus	Berriasian	Barremian	Dicraeosauridae	—
Amargatitanis	Barremian	Barremian	Titanosauria	Apesteguía 2007
Amazonsaurus	Aptian	Albian	Diplodocoidea	Carvalho *et al*. 2003
Ammosaurus	Pliensbachian	Toarcian	Prosauropoda	—
Ampelosaurus	L. Campanian	E. Maastrichtian	Lithostrotia	—
Amphicoelias	Kimmeridgian	Tithonian	Diplodocoidea	—
Amygdalodon	Bajocian	Bajocian	Eusauropoda	—
Anchisaurus	Pliensbachian	Toarcian	Prosauropoda	—
Andesaurus	Albian	Turonian	Titanosauria	—
Antarctosaurus	Campanian	Maastrichtian	Nemegtosauridae	Wilson 2005a
Antetonitrus	Norian	Norian	Sauropoda	Yates & Kitching 2003
Apatosaurus	Kimmeridgian	Tithonian	Diplodocidae	—
Aragosaurus	L. Hauterivian	E. Barremian	Eusauropoda	—
Archaeodontosaurus	Bathonian	Bathonian	Eusauropoda	Buffetaut 2005
Argentinosaurus	Albian	Turonian	Titanosauria	—
Argyrosaurus	Campanian	Maastrichtian	Titanosauria	—
Asylosaurus	L. Carnian	Rhaetian	Sauropodomorpha	Galton 2007
Atlasaurus	Bathonian	Callovian	Macronaria	—
Australodocus	Tithonian	Tithonian	Diplodocidae	Remes 2007

Austrosaurus	L. Albian	L. Albian	Titanosauria	—
Barapasaurus	Pliensbachian	Toarcian	Eusauropoda	—
Barosaurus	Kimmeridgian	Tithonian	Diplodocidae	—
Baurutitan	L. Maastrichtian	L. Maastrichtian	Lithostrotia	Kellner et al. 2005
Bellusaurus	Aalenian	Callovian	Macronaria	—
Blikanasaurus	E. Norian	E. Norian	Sauropoda	—
Bonatitan	Campanian	Maastrichtian	Saltasauridae	Martinelli & Forasiepi 2004
Bonitasaura	Santonian	Santonian	Nemegtosauridae	Apesteguía 2004
Borealosaurus	Cenomanian	Turonian	Opisthocoelicaudiinae	You *et al*. 2004
Brachiosaurus	Kimmeridgian	Tithonian	Brachiosauridae	—
Brachytrachelopan	Tithonian	Tithonian	Dicraeosauridae	Rauhut *et al*. 2005
Camarasaurus	Kimmeridgian	Tithonian	Macronaria	—
Camelotia	Rhaetian	Rhaetian	Sauropoda	Upchurch et al. 2007a; Yates 2007
Cardiodon	L. Bathonian	L. Bathonian	Sauropoda	—
Cathartesaura	Cenomanian	Coniacian	Rebbachisauridae	Gallina & Apesteguía 2005
Cedarosaurus	Barremian	Barremian	Brachiosauridae	—
Cetiosauriscus	Callovian	Callovian	Eusauropoda	Heathcote & Upchurch 2003; Rauhut *et al*. 2005
Cetiosaurus	L. Bajocian	L. Bathonian	Eusauropoda	—
Chebsaurus	Aalenian	Callovian	Eusauropoda	Mahammed *et al*. 2005
Chinshakiangosaurus	Hettangian	Toarcian	Sauropoda	Upchurch *et al*. 2007b
Chuanjiesaurus	Aalenian	Bajocian	Sauropoda	—
Chubutisaurus	Albian	Albian	Titanosauria	—
Coloradisaurus	Norian	Norian	Prosauropoda	—
Daanosaurus	Oxfordian	Tithonian	Macronaria	Ye *et al*. 2005
Dashanpusaurus	Bajocian	Callovian	Eusauropoda	Peng *et al*. 2005
Datousaurus	Bathonian	Callovian	Sauropoda	—
Dicraeosaurus	Kimmeridgian	Tithonian	Dicraeosauridae	—
Dinheirosaurus	Kimmeridgian	Kimmeridgian	Diplodocoidea	—
Diplodocus	Kimmeridgian	Tithonian	Diplodocidae	—

Dongbeititan	Barremian	Barremian	Somphospondyli	Wang *et al*. 2007
Dongyangosaurus	Cenomanian	Maastrichtian	Titanosauriformes	Lü *et al*. 2008a
Efraasia	M. Norian	M. Norian	Sauropodomorpha	Yates 2003b, 2007
Eomamenchisaurus	Aalenian	Callovian	Eusauropoda	Lu *et al*. 2008b
Epachthosaurus	Cenomanian	Turonian	Titanosauria	—
Erketu	Aptian	Albian	Somphospondyli	Ksepka & Norell 2006
Eucnemesaurus	Norian	Norian	Sauropodomorpha	Yates 2006
Euhelopus	Tithonian	Aptian	Somphospondyli	Wilson & Upchurch 2009
Europasaurus	M. Kimmeridgian	M. Kimmeridgian	Macronaria	Sander *et al*. 2006
Ferganasaurus	Callovian	Callovian	Neosauropoda	Alifanov & Averianov 2003
Fusuisaurus	Aptian	Albian	Titanosauriformes	Mo *et al*. 2006
Futalognkosaurus	L. Turonian	E. Coniacian	Lithostrotia	Calvo *et al*. 2007
Galveosaurus	Tithonian	Tithonian	Turiasauria	Sanchez-Hernandez 2005
Glacialisaurus	Sinemurian	Pliensbachian	Sauropodomorpha	Smith & Pol 2007
Gobititan	Albian	Albian	Titanosauria	You *et al*. 2003
Gondwanatitan	Turonian	Santonian	Lithostrotia	—
Gongxianosaurus	Hettangian	Toarcian	Sauropoda	—
Haplocanthosaurus	Kimmeridgian	Tithonian	Macronaria	—
Huabeisaurus	Campanian	Campanian	Titanosauria	—
Huanghetitan	Berriasian	Albian	Titanosauriformes	You *et al*. 2006
Hudiesaurus	Tithonian	Tithonian	Eusauropoda	—
Isanosaurus	L. Norian	Rhaetian	Sauropoda	—
Isisaurus	Maastrichtian	Maastrichtian	Lithostrotia	Wilson & Upchurch 2003
Jainosaurus	Maastrichtian	Maastrichtian	Nemegtosauridae	Wilson 2005a
Janenschia	Tithonian	Tithonian	Titanosauria	—

Jiangshanosaurus	Albian	Albian	Lithostrotia	—
Jingshanosaurus	Hettangian	Pliensbachian	Sauropoda	—
Jiutaisaurus	Aptian	Aptian	Titanosauriformes	Wu *et al*. 2006; Wang *et al*. 2007
Jobaria	Berriasian	Hauterivian	Eusauropoda	Wilson & Upchurch 2009
Karongasaurus	Aptian	Aptian	Titanosauria	Gomani 2005
Klamelisaurus	Aalenian	Callovian	Sauropoda	—
Kotasaurus	Pliensbachian	Toarcian	Sauropoda	—
Lamplughsaura	Sinemurian	Sinemurian	Sauropoda	Kutty *et al*. 2007
Laplatasaurus	Campanian	Maastrichtian	Lithostrotia	—
Lapparentosaurus	Bathonian	Bathonian	Titanosauriformes	—
Lessemsaurus	Norian	Norian	Sauropoda	Upchurch et al. 2007a; Yates 2007
Ligabuesaurus	L. Aptian	Albian	Titanosauria	Bonaparte *et al*. 2006
Limaysaurus	Albian	Turonian	Rebbachisauridae	Salgado *et al*. 2004
Lirainosaurus	L. Campanian	L. Campanian	Lithostrotia	—
Losillasaurus	M. Tithonian	E. Berriasian	Turiasauria	Royo-Torres *et al*. 2006
Lourinhasaurus	Kimmeridgian	Tithonian	Eusauropoda	—
Lufengosaurus	Hettangian	Sinemurian	Prosauropoda	—
Lusotitan	L. Kimmeridgian	Tithonian	Brachiosauridae	Antunes & Mateus 2003
Magyarosaurus	L. Maastrichtian	L. Maastrichtian	Lithostrotia	—
Malawisaurus	Aptian	Aptian	Lithostrotia	—
Mamenchisaurus	Oxfordian	Tithonian	Eusauropoda	—
Massospondylus	Hettangian	Sinemurian	Prosauropoda	—
Maxakalisaurus	Campanian	Maastrichtian	Titanosauria	Kellner *et al*. 2006
Melanorosaurus	Norian	Norian	Sauropoda	Yates 2007
Mendozasaurus	L. Coniacian	L. Santonian	Lithostrotia	González Riga 2003
Mongolosaurus	Berriasian	Albian	Titanosauria	Wilson 2005a; Mannion in press
Mussaurus	Norian	Norian	Sauropodomorpha	Upchurch *et al*. 2007a; Yates 2007

Muyelensaurus	Turonian	Coniacian	Lithostrotia	Calvo *et al*. 2008
Nemegtosaurus	E. Maastrichtian	E. Maastrichtian	Nemegtosauridae	Wilson 2005a
Neuquensaurus	Campanian	Maastrichtian	Saltasauridae	—
Nigersaurus	Aptian	Cenomanian	Rebbachisauridae	—
Nopcsaspondylus	Coniacian	Coniacian	Rebbachisauridae	Apesteguía 2007
Ohmdenosaurus	M. Toarcian	M. Toarcian	Sauropoda	—
Omeisaurus	Bathonian	Callovian	Eusauropoda	—
Opisthocoelicaudia	E. Maastrichtian	E. Maastrichtian	Opisthocoelicaudiinae	—
Oplosaurus	Barremian	Barremian	Macronaria	—
Ornithopsis	Barremian	Barremian	Titanosauriformes	—
Paluxysaurus	L. Aptian	E. Albian	Titanosauriformes	Rose 2007
Pantydraco	Rhaetian	Hettangian	Sauropodomorpha	Galton *et al*. 2007
Paralititan	Cenomanian	Cenomanian	Lithostrotia	—
Patagosaurus	Callovian	Callovian	Eusauropoda	—
Pellegrinisaurus	Campanian	E. Maastrichtian	Lithostrotia	—
Pelorosaurus	L. Berriasian	Valanginian	Titanosauriformes	—
Phuwiangosaurus	Valanginian	Hauterivian	Titanosauria	—
Plateosauravus	Norian	Norian	Sauropodomorpha	Yates 2003a, 2007
Plateosaurus	Norian	Norian	Prosauropoda	—
Pleurocoelus	E. Aptian	E. Aptian	Titanosauriformes	—
Pradhania	Sinemurian	Sinemurian	Sauropodomorpha	Kutty *et al*. 2007
Puertasaurus	E. Maastrichtian	E. Maastrichtian	Lithostrotia	Novas *et al*. 2005
Qingxiusaurus	Cenomanian	Maastrichtian	Titanosauria	Mo *et al*. 2008
Quaesitosaurus	M. Campanian	M. Campanian	Nemegtosauridae	—
Rapetosaurus	Campanian	Maastrichtian	Nemegtosauridae	—
Rayososaurus	Aptian	Aptian	Rebbachisauridae	—
Rebbachisaurus	Albian	Albian	Rebbachisauridae	—
Rhoetosaurus	Bajocian	Bajocian	Eusauropoda	—
Rinconsaurus	L. Turonian	Coniacian	Saltasauridae	Calvo & González Riga 2003
Riojasaurus	Norian	Norian	Prosauropoda	—
Rocasaurus	L. Campanian	E. Maastrichtian	Lithostrotia	—
Ruehleia	Norian	Norian	Sauropodomorpha	Upchurch *et al*. 2007a; Yates 2007
Saltasaurus	L. Campanian	E. Maastrichtian	Saltasauridae	—

Sanpasaurus	Hettangian	Toarcian	Sauropoda	P. Upchurch pers. comm. 2007
Saturnalia	Carnian	Carnian	Sauropodomorpha	—
Sauroposeidon	Aptian	Albian	Brachiosauridae	—
Shunosaurus	Bathonian	Callovian	Eusauropoda	—
Sonidosaurus	Turonian	Maastrichtian	Titanosauria	Xu *et al*. 2006
Supersaurus	Kimmeridgian	Tithonian	Diplodocidae	Lovelace *et al*. 2008
Suuwassea	L. Kimmeridgian	Tithonian	Flagellicaudata	Harris & Dodson 2004
Tangvayosaurus	Aptian	Albian	Titanosauria	—
Tastavinsaurus	E. Aptian	E. Aptian	Titanosauriformes	Canudo *et al*. 2008
Tazoudasaurus	Toarcian	Toarcian	Sauropoda	Allain *et al*. 2004
Tehuelchesaurus	Tithonian	Tithonian	Eusauropoda	—
Tendaguria	Tithonian	Tithonian	Sauropoda	—
Thecodontosaurus	L. Carnian	Rhaetian	Sauropodomorpha	Upchurch *et al*. 2007a; Yates 2007
Tornieria	Tithonian	Tithonian	Diplodocidae	—
Trigonosaurus	L. Maastrichtian	L. Maastrichtian	Lithostrotia	Campos *et al*. 2005
Turiasaurus	Tithonian	E. Berriasian	Turiasauria	Royo-Torres *et al*. 2006
Uberabatitan	Maastrichtian	Maastrichtian	Lithostrotia	Salgado & Carvalho 2008
Unaysaurus	Carnian	Norian	Prosauropoda	Leal *et al*. 2004
Venenosaurus	Barremian	Barremian	Titanosauria	—
Volkheimeria	Callovian	Callovian	Eusauropoda	—
Vulcanodon	Toarcian	Toarcian	Sauropoda	—
Xenoposeidon	Berriasian	Berriasian	Macronaria	Taylor & Naish 2007
Yimenosaurus	Pliensbachian	Toarcian	Prosauropoda	—
Yuanmousaurus	Aalenian	Callovian	Eusauropoda	Lü *et al*. 2006
Yunnanosaurus	Hettangian	Sinemurian	Prosauropoda	—
Zapalasaurus	L. Barremian	E. Aptian	Rebbachisauridae	Salgado *et al*. 2006

Basal sauropodomorphs and prosauropods

The basal sauropodomorph phylogeny presented by Galton and Upchurch (2004) has been superseded by the more recent analyses of Yates (2007) and Upchurch *et al*. (2007a). These latter analyses recovered a basal sauropodomorph grade comprised of *Saturnalia*, *Thecodontosaurus*, *Pantydraco*, *Mussaurus*, *Plateosauravus*, *Ruehleia* and *Efraasia*. Although there is some disagreement in terms of the monophyly of the prosauropods (see 'Chapter 1: Introduction to the Sauropodomorpha'), this work has followed the analysis of Upchurch *et al*. (2007a) in that taxa have still been included in a prosauropod clade (i.e. *Ammosaurus*, *Anchisaurus*, '*Gyposaurus*', *Coloradisaurus*, *Plateosaurus*, *Riojasaurus*, *Lufengosaurus*, *Massospondylus*, *Plateosauravus* and *Yunnanosaurus*). Additionally, several taxa previously considered 'traditional' prosauropods (e.g. in Galton and Upchurch 2004) have been recovered as basal sauropods in these two recent analyses (i.e. *Camelotia*, *Jingshanosaurus*, *Lessemsaurus* and *Melanorosaurus*).

Three sauropodomorph taxa listed as valid in Galton and Upchurch (2004) are now considered invalid. Yates (2003a, 2006) proposed that *Euskelosaurus* was invalidated and referred many of the remains previously referred to this taxon to the resurrected genera *Plateosauravus* and *Eucnemesaurus*. Similarly, Yates (2003b) considered *Sellosaurus* a *nomen dubium*, and referred material formerly referable to this genus to *Efraasia* and a new species combination of *Plateosaurus* (*P. gracilis*). Gauffre (1993a) named a second species of *Melanorosaurus* (*M. thabanensis*) based on an isolated femur from the Early Jurassic of Lesotho. Yates (2007) recently expressed doubt as to the validity of this second species, and also noted that one of the characters used to link the two species was actually more widespread throughout Sauropoda. As a result, this second species has been removed from the genus *Melanorosaurus* and is included in the analysis as Sauropoda indet.

Azendohsaurus was named for a dentary from the Late Triassic of Morocco. Originally described as an ornithischian (Dutuit 1972), it was later reinterpreted by Galton (1990), and then re-described by Gauffre (1993b), as a prosauropod. More recent work, however, has demonstrated that it represents a non-dinosaurian archosauriform (Jalil and Knoll 2002; Irmis *et al*. 2007).

For the purposes of this study several prosauropod taxa have been restricted to their holotype specimens. Pending re-study of referred material (Barrett *et al*. 2005, 2007), *Lufengosaurus huenei* and *Yunnanosaurus huangi* have both been restricted to their holotype specimens (IVPP V15 and NGMJ 004546 respectively). The taxon listed as '*Gyposaurus*' *sinensis* is restricted to the specimen mounted in the NGMJ (formerly V43), which was included in the phylogenetic analysis of Upchurch *et al*. (2007a). Although this specimen has often been referred to *Lufengosaurus* (Galton 1990), Upchurch *et al*. (2007a) suggested that it represents a distinct taxon.

As mentioned above, *Yunnanosaurus huangi* is a prosauropod from the Early Jurassic (Hettangian-Sinemurian) of China. Lü *et al*. (2007a) recently named a second species (*Y. youngi*) from the Middle Jurassic of China. As this new species cannot be dated with any more accuracy than 'Middle Jurassic', the stratigraphic range of *Yunnanosaurus* could extend from the Hettangian until the Callovian, traversing almost 40 million years. As there is some doubt as to the relationships between these two species (and the 'diagnostic' feature listed as uniting them is more widespread among sauropodomorphs), each will be entered as a separate taxon to avoid extending stratigraphic ranges where neither species has been found. Furthermore, it is not entirely clear from the description of Lü *et al*. (2007a) that "*Yunnanosaurus*" *youngi* represents a prosauropod.

Basal sauropods

Royo-Torres *et al*. (2006) erected a new clade within Eusauropoda which they named Turiasauria. They included the new taxon *Turiasaurus*, and also *Galveosaurus*, within this clade as well as *Losillasaurus*, a sauropod previously suggested to have diplodocoid affinities (Casanovas *et al*. 2001).

The various Middle Jurassic Madagascan material described as '*Bothriospondylus madagascariensis*' (Lydekker 1895; Boule 1896; Thevenin 1907; Lavocat 1955a-c, 1957) is considered to represent a non-neosauropod eusauropod (Läng and Goussard 2007; Mannion 2010), although the material does not constitute a valid taxon. The phylogenetic position of the contemporaneous Madagascan sauropod *Archaeodontosaurus* (Buffetaut 2005) is modified to place it as a basal eusauropod, following Upchurch *et al*. (2007b).

Dong (1997) coined the name *Hudiesaurus* for a vertebra and forelimb (as well as teeth) of a Late Jurassic Chinese sauropod. Dong (1997, p. 104) stated that although the right forelimb was collected from the same horizon as the vertebra, 'the quarry is about 1.1km from the quarry of the type specimen'. Based on a lack of overlapping material (and lack of association), the forelimb and teeth cannot be assigned to the same taxon as the vertebra. Therefore, the name *Hudiesaurus* has been restricted to just the vertebra, with the forelimb considered a separate individual and included as Eusauropoda indet. (Upchurch and Mannion in prep).

Two Chinese taxa considered *nomen dubia* by Upchurch *et al*. (2004a) are deemed valid in this study. Upchurch *et al*. (2007b) restudied *Chinshakiangosaurus* and found it to be a diagnostic basal sauropod, while *Sanpasaurus* is also revalidated and is considered a basal sauropod (P. Upchurch pers. comm. 2007).

Peng *et al*. (2005) named a new Chinese 'camarasaurid' (*Dashanpusaurus*). However, this lacks camarasauromorph or macronarian features and cannot be placed beyond

Eusauropoda based on a lack of opisthocoely in the posterior dorsals (excluding it from Macronaria) and the absence of procoelous proximal caudal vertebrae (excluding it from Flagellicaudata and Titanosauria). Additionally, the transverse width of the proximal end of the tibia appears greater than that of the anteroposterior length, characteristic of derived non-neosauropod eusauropods (Mannion 2010).

The material Huene (1922) originally described as '*Cetiosauriscus*' *greppini* is considered a diagnostic basal eusauropod and requires a new name (Schwarz *et al*. 2007). The English taxon *Cetiosauriscus* has previously been provisionally regarded as a putative diplodocoid (Upchurch *et al*. 2004a), but is here considered a non-neosauropod eusauropod (Heathcote and Upchurch 2003; Rauhut *et al*. 2005).

Upchurch *et al*. (2004a) retained *Dystrophaeus* as a valid taxon despite its apparent lack of autapomorphies. Recent re-examination, however, has demonstrated it to be an undiagnostic eusauropod (P. Upchurch pers. comm. 2008).

Jobaria was described by Sereno *et al*. (1999) as a non-neosauropod eusauropod, based on several features cited as plesiomorphic (though most of these have been demonstrated to not be related to neosauropod synapomorphies; Upchurch *et al*. 2004a). Wilson (2002) and Rauhut *et al*. (2005) also recovered it as a non-neosauropod eusauropod; however, Upchurch *et al*. (2004a) recovered *Jobaria* as a basal macronarian (in a clade with *Bellusaurus* and *Atlasaurus*). Royo-Torres *et al*. (2006) used the data matrix of Upchurch *et al*. (2004a) in their analysis of *Turiasaurus*. As well as recovering the clade of turiasaurs discussed earlier, their analysis also placed *Jobaria* (and also, interestingly, *Atlasaurus* but not *Bellusaurus*) as a non-neosauropod eusauropod. Wilson and Upchurch (2009) re-ran the Upchurch *et al*. (2004a) analysis using revised scorings for *Euhelopus*, though with no other alterations; the strict reduced consensus tree recovered *Jobaria* as a non-neosauropod eusauropod. In addition, recent work by Rauhut and López-Arbarello (2009) has argued for a Middle Jurassic age for *Jobaria*,

which would be congruent with its position as a more basal sauropod. Following these analyses, *Jobaria* is here considered a non-neosauropod eusauropod.

Lapparent (1960) described numerous remains from a large number of localities throughout the Saharan region of Africa (including Niger and Algeria). These remains were described as '*Rebbachisaurus tamesnensis*', although no type material was designated, nor were any diagnostic features listed. Though listed as being recovered from the same locality as *Jobaria*, Sereno *et al*. (1999) never actually referred any of this material to their new taxon although, somewhat confusingly, Upchurch *et al*. (2004a) referred the '*R*. *tamesnensis*' material to *Nigersaurus*. The material described by Lapparent (1960) is extremely fragmentary and consists largely of isolated elements. It is possible the material is composed of elements belonging to both *Jobaria* and *Nigersaurus*; however, as no shared autapomorphies can be recognised this cannot be demonstrated. Additionally, the poor quality of the material makes referral to any sauropod clade extremely difficult; thus the material comprising '*R*. *tamesnensis*' has been considered as Sauropoda indet.

Diplodocoids

Harris and Dodson (2004) named a new node-based clade (Flagellicaudata) for the most recent common ancestor of *Diplodocus* and *Dicraeosaurus* and all of its descendants; this clade name will be utilised throughout this study.

Filla and Redman (1994) described a relatively complete Late Jurassic sauropod from the Morrison Formation of Wyoming as a new basal species of *Apatosaurus* (*A. yahnahpin*), though Bakker (1998) later proposed that this taxon was a distinct genus and coined the new name '*Eobrontosaurus*'. Upchurch *et al*. (2004a) suggested that it was actually a junior synonym of *Camarasaurus*; however re-examination of the material (PALEON 001) has demonstrated its diplodocid affinities, although it is not considered a distinct

taxon in this analysis (awaiting restudy and description of new materials; R. Bakker pers. comm. 2008).

The diplodocid *Dyslocosaurus* was named by McIntosh *et al*. (1992) based on diagnostic limb material from Wyoming, USA. However, this specimen was recorded as having been collected from the late Maastrichtian Lance Formation, although McIntosh *et al*. (1992) argued that its preservation and diplodocid affinities indicated that this provenance was incorrect, with a Late Jurassic Morrison Formation provenance suggested instead. The authors conceded that no conclusive decision could be reached regarding the specimen's age; consequently, this taxon has been omitted from these analyses rather than extending its temporal span from the Kimmeridgian through to the end-Cretaceous (a time-span of 90 Myr).

'*Seismosaurus*' is considered to be a junior synonym of *Diplodocus longus*, as the only apparently diagnostic feature (the hook-shaped distal end of the ischium; Upchurch *et al*. 2004a) was actually part of a neural spine adhered to the ischium (Lucas *et al*. 2006; Lovelace *et al*. 2008).

Doubt has been expressed as to the validity of the diplodocid *Supersaurus* in the past (e.g. Gillette 1994) but, based on a new, more complete specimen, it has been demonstrated to be a valid taxon (Lovelace *et al*. 2008; pers. obs. 2008).

Upchurch *et al*. (2004b) accepted previous referral of '*Elosaurus parvus*' (CM 566) to the genus *Apatosaurus* (McIntosh 1981); however, they considered it distinct at the specific level. Along with a second individual (UWGM 15556), *Apatosaurus parvus* is considered valid.

Material originally described as '*Rebbachisaurus tessonei*' (Calvo and Salgado 1995), and then referred to *Rayososaurus* (Wilson and Sereno 1998), is included as a valid taxon:

Limaysaurus (Salgado *et al*. 2004). Following Sereno *et al*. (2007), the taxa *Zapalasaurus* and '*Histriasaurus*' are also considered rebbachisaurids, though the latter is not included as a valid taxon.

Basal macronarians

Ye *et al*. (2005) described a new sauropod (*Daanosaurus*) from China as a brachiosaurid; however, this specimen cannot be assigned beyond Macronaria, based on the presence of opisthocoelous posterior dorsals coupled with unbridged proximal chevrons.

'*Apatosaurus minimus*' (Mook 1917) is referred to the Macronaria based on features of the pelvic girdle, and is retained as a valid taxon (following Upchurch *et al*. 2004a), pending restudy. Several indeterminate North American specimens previously referred to *Haplocanthosaurus* (e.g. USNM 4264 and 4275; McIntosh and Williams 1988) have been removed from this genus (on the basis of a lack of shared diagnostic features) and referred to various less inclusive sauropod clades (e.g. Macronaria, Diplodocidae, Eusauropoda, etc.).

The recently named British sauropod, *Xenoposeidon*, has been retained as a valid taxon (although a number of the listed autapomorphies are more widespread in sauropods, or are based on misinterpretations, and future studies may show it to be a *nomen dubium*). Although Taylor and Naish (2007) described it as a neosauropod (and even went so far as to suggest it may represent a new neosauropod family), it is here placed within Macronaria based on the (probable) possession of an opisthocoelous centrum in a posterior dorsal (though see *Supersaurus* for a diplodocid with a similar condition).

Titanosauriforms

Many specimens described as brachiosaurids in the literature have been included in the analysis at the slightly less inclusive clade of Titanosauriformes, based on a lack of brachiosaurid synapomorphies. In particular this has been applied to individual teeth which have been described as brachiosaurids, whereas usually they cannot be distinguished from basal titanosaur teeth (see Barrett *et al*. 2002; Barrett and Wang 2007).

The Chinese titanosauriform *Huanghetitan liujiaxiaensis* was named by You *et al*. (2006) for a specimen dated as Early Cretaceous (an epoch spanning 46 million years). A second species was erected (*H. ruyangensis*; Lü *et al*. 2007b) based on early Late Cretaceous remains, thereby extending the temporal range even further. However, there is some doubt as to the relationship of these species and, as with *Yunnanosaurus* (see above), each has been considered a separate taxon to avoid extending stratigraphic ranges where neither species has been found.

The phylogenetic position of the Chinese taxon *Euhelopus* has proved controversial, with some analyses (Upchurch 1995, 1998, 1999; Upchurch *et al*. 2004a) placing it outside Neosauropoda and other studies (Wilson and Sereno 1998; Wilson 2002; Curry Rogers 2005) recovering it as the sister taxon to Titanosauria (with this clade named Somphospondyli; Wilson and Sereno 1998). Re-examination of the specimen, however, has ended this controversy, with *Euhelopus* recovered as a somphospondyl (Wilson and Upchurch 2009). Additionally, this work has suggested that *Euhelopus*, *Erketu* and teeth from China (Barrett and Wang 2007) and Spain (Canudo *et al*. 2002) may all form a clade of basal titanosaurs (‘euhelopodids’).

Wang *et al*. (2007) placed *Dongbeititan* in the Somphospondyli, describing it as a basal titanosauriform more derived than *Euhelopus*, *Fusuisaurus* and *Huanghetitan*, but less derived than *Jiutaisaurus* and *Gobititan*, a position supported here.

Wilson and Upchurch (2003) found the type species of '*Titanosaurus*' ('*T. indicus*') to be invalid and thus the genus and its co-ordinated rank-taxa can no longer be used. The taxonomy and systematics of '*Titanosaurus*' and its rank-taxa thus follows the work of these authors. Five species of '*Titanosaurus*' were considered valid by Wilson and Upchurch (2003): three of these already had new generic names (*Neuquensaurus*, *Magyarosaurus* and *Laplatasaurus*) and they re-named '*T. colberti*' as *Isisaurus*. The fifth diagnostic species of '*Titanosaurus*' (DGM 'Series C'; Powell 1987) has since been named *Baurutitan* (Kellner *et al*. 2005). The co-ordinated rank-taxa (i.e. Titanosaurinae, Titanosauridae and Titanosauroidea) have thus been abandoned, although the unranked taxon Titanosauria remains valid. Lithostrotia (Upchurch *et al*. 2004a) is now used for more derived titanosaurs.

Ostrom (1970) described abundant sauropod material from the Early Cretaceous Cloverly Formation of North America and tentatively suggested titanosaur affinities. Re-examination of the material has confirmed that some elements do represent titanosaurs, whereas other material cannot be assigned beyond the less inclusive Titanosauriformes. The only associated material (YPM 5449) may be diagnostic (M. Wedel pers. comm. 2008), though it is possible that it will prove to be synonymous with *Paluxysaurus* (M. D'Emic pers. comm. 2008). For the purposes of this study, however, the 'Cloverly titanosaur' is considered a distinct taxon and is restricted to YPM 5449.

Numerous undescribed sauropod remains have been excavated from the Early Cretaceous Dalton Wells Quarry of North America (Britt *et al*. 1996, 1997, 1998; 2004; Eberth *et al*. 2006). Although originally listed as also containing a 'camarasaurid', there does not seem to be any strong basis for this, and the majority of material seems to show titanosaur affinities, with the remaining specimens considered indeterminate brachiosaurids, and not referable to *Cedarosaurus* (contra Eberth *et al*. 2006).

Numerous titanosaurian remains from Pakistan have recently been described as new taxa ('*Pakisaurus*', '*Sulaimanisaurus*', '*Khetranisaurus*', '*Marisaurus*' and '*Balochisaurus*'; Malkani 2006, and references therein); however, none of these are based on diagnostic material and most are represented by fragmentary, disarticulated remains. Thus, all of these Pakistani taxa are regarded as *nomen dubia* and are included as Titanosauria indet.

McIntosh (1990) named the stem-based clade Opisthocoelicaudiinae for all saltasaurids more closely related to *Opisthocoelicaudia* than to *Saltasaurus* (Wilson and Upchurch 2003). You *et al*. (2004) recently referred the genus *Borealosaurus* to this clade and Barsbold *et al*. (2007) mentioned a newly discovered Late Cretaceous Mongolian sauropod which, based on opisthocoelous anterior caudals, has also been included within this clade.

There has been much discussion (Yu 1993; Upchurch 1995, 1998, 1999; Calvo 1994; Salgado and Calvo 1997; Wilson 2002, 2005a; Curry Rogers and Forster 2001; Upchurch *et al*. 2004a; Curry Rogers 2005) of the phylogenetic position of nemegtosaurid sauropods (*Nemegtosaurus* and *Quaesitosaurus* being the two taxa originally described as comprising Nemegtosauridae; Upchurch 1995), with both diplodocoid and titanosaur affinities suggested. However, following the work of Wilson (2005a), there is now general agreement that nemegtosaurids represent a clade of derived titanosaurs. Apesteguía (2004) placed the new taxon *Bonitasaura* within Nemegtosauridae and Wilson (2005a) also referred several other existing taxa to this clade (*Jainosaurus*, *Antarctosaurus* and *Rapetosaurus*). Wilson (2005a) also revalidated *Mongolosaurus* and noted that it possessed a possible nemegtosaurid synapomorphy: its validity is supported here, although there remains doubt as to its exact position within Titanosauria (Mannion, in press). Other putative nemegtosaurids (e.g. *Phuwiangosaurus*; Martin *et al*. 1999) have also been retained within the less inclusive Titanosauria, based on a lack of nemegtosaurid synapomorphies. Following Wilson

(2005a), Nemegtosauridae is here phylogenetically defined as the stem-based clade including all titanosaurs more closely related to *Nemegtosaurus* than to *Saltasaurus*.

METHODOLOGICAL APPROACHES

Assessing numbers of individuals and localities

Accurate estimation of the number of individual fossil organisms is often problematic, especially when dealing with fragmentary vertebrate remains. For this study the minimum number of individuals (MNIs) has been estimated for each locality. The use of MNIs is a standard tool in archaeological, palaeoecological and taphonomic studies (e.g. Grayson 1973; Badgley 1986; Gilinsky and Bennington 1994; Davis and Pyenson 2007). For example, if a quarry consisted of closely associated material belonging to the same taxon, with no duplication or size variation of elements, then this would be considered to represent a single individual. However, this method of estimating the MNIs does have the disadvantage of unavoidably undercounting the number of individuals. Estimating the number of individual organisms present at a given locality can be much more difficult when dealing with trackways because a single trackmaker could have made many different tracks, and the relative size of foot impressions can be affected by under-printing and over-printing (Day *et al*. 2002, 2004; Milàn and Bromley 2006). The MNIs was estimated for each tracksite based on information in the description of the tracksite. If insufficient information was available, then a tracksite was assumed to represent no more than one trackmaker per recognisable taxon. This assumption was made even when an author stated that a locality had produced 'trackways' (e.g. Lockley *et al*. 2006).

Locality-based estimates avoid the problems concerning the estimation of number of individuals (particularly for trackway data), but one problem with this approach is that the boundaries between 'separate' localities can be somewhat arbitrary. For example, areas such as Como Bluff in the Late Jurassic Morrison Formation of North America have produced sauropod material from approximately the same horizons in several closely situated quarries (Ostrom and McIntosh 1966). In this study, localities are based on the

divisions used in recent datasets (e.g. Lockley *et al*. 1994; Weishampel *et al*. 2004a; www.paleodb.org; Carrano 2008b) and defined as: separate geographic locations and discrete stratigraphic levels that yield body fossils and/or trackways (modified from Lockley *et al*. 1994: p. 234). Each locality is counted only once, irrespective of the number of individuals present. However, there are a number of instances where many tracksites, although discrete from one another, are in extremely close proximity to each other (e.g. in the Republic of Korea). In the above classification these have all been treated as separate entities; however, it is possible that these might be oversplit and may just reflect a lack of preservation in between tracksites (and thus numbers of tracksites may be over-estimated). To attempt to counter this potential problem, tracksites have also been considered based on geographical region (e.g. state), following Farlow (1992), so that only one tracksite is represented per region for each time bin. Although this method will undoubtedly under-estimate the number of distinct tracksites, it is hoped that the use of both approaches for determining numbers of tracksites will ameliorate the problems of each method.

Environmental associations

Only the Jurassic-Cretaceous sauropod element of the database has been utilised for this analysis because most tracks assigned to basal sauropodomorphs are of dubious affinity and this analysis is based in part on a comparison of body fossils and trackways. This sauropod dataset was further filtered to remove those occurrences that cannot be identified more precisely than 'Sauropoda indet.'. Such indeterminate occurrences were removed because they cannot help to resolve environmental associations within Sauropoda, and would inevitably introduce considerable noise into the dataset. The resulting dataset consists of information on 896 localities, comprising 706 body fossil localities and 190 tracksites. These localities are estimated to represent approximately 1988 sauropod individuals (1355 based on body fossils and 633 trackmakers).

Environmental categories

The depositional environments that have yielded body fossils and trackways have been allocated to one of two broad categories: 'inland' and 'coastal'. Sauropod fossils are occasionally recovered from marine deposits (0.01% of occurrences), but these have been excluded from this study because it seems highly unlikely that sauropods could have lived in marine environments. Inland environments include fluvial, lacustrine, floodplain and aeolian settings; coastal environments comprise estuarine, deltaic, lagoonal and carbonate platform settings. This partition is admittedly crude and it is possible that any correlations recovered could actually reflect more subtle preferences, such as one group preferring more arid conditions. Additionally, some of the fluvial settings could be situated close to the coastline, but have only ever been recorded as representing 'fluvial' and thus here have been incorporated into the inland category. It is also possible that these environmental categories may have very different preservational potentials for trackways and body fossils. However, there is not enough information available in the palaeontological literature to allow environmental analyses

on a finer scale. Furthermore, the focus is on the inland/coastal division because these categories have yielded environmental associations among other dinosaurs (Butler *et al*. 2007; Butler and Barrett 2008) and because previous studies of sauropod palaeoecology have made claims concerning preferences for one of these broad habitat types (e.g. Lehman 1987; Lucas and Hunt 1989).

Taxonomic categories

The search for environmental associations within Sauropoda requires that the data are divided into at least two distinct types or categories. At present, most sauropod trackways can only be placed in one of two (or perhaps three) broad categories: i.e. narrow-gauge and wide-gauge with, and without, manus-claw and phalangeal impressions (Fig. 2.1: Farlow *et al*. 1989; Lockley *et al*. 1994; Wilson and Carrano 1999; Day *et al*. 2004). Narrow-gauge trackways have footprints that approach (or intersect) the midline, with pollex claw impressions preserved (e.g. *Parabrontopodus*: Fig. 2.1A), whereas wide-gauge trackways have footprints placed well away from the midline and pollex claw impressions are frequently absent (e.g. *Brontopodus*: Fig. 2.1B). Wilson and Carrano (1999) argued that titanosaurs were responsible for producing these wide-gauge tracks, based on several femoral morphological features (such as the lateral deflection of the proximal one-third of the femur) which suggest that titanosaurs held their limbs further from the midline of the animal than did other sauropods (Fig. 2.1C, D). This interpretation is also supported by the derived loss of pollex claws and manual phalanges in both titanosaurian skeletal remains and many wide-gauge trackways (Salgado *et al*. 1997; Day *et al*. 2002), though this may not be the case in basal titanosaurs or the more inclusive Titanosauriformes (Day *et al*. 2004). However, Henderson (2006) argued against a titanosaurian origin for wide-gauge tracks. He modelled the position of the centre of mass in two walking sauropods (note that no titanosaurs were included in his analysis) and found that *Brachiosaurus* and *Diplodocus* were only stable with a wide-gauge and narrow-gauge stance, respectively. Henderson

(2006) proposed that all large sauropods (over 12.6 tonnes) would have been constrained to adopt a wide-gauge stance in order to maintain stability during locomotion, meaning that many large non-titanosaurian taxa would have produced wide-gauge trackways. However, many large-bodied non-titanosaurian sauropods lack most or all of the morphological modifications which Wilson and Carrano (1999) identified as adaptations for a wide-gauge stance (see above). Furthermore, the almost complete absence of narrow-gauge tracks in the Cretaceous (when titanosauriforms comprised the vast majority of sauropods), coupled with the extreme size reduction of many sauropods (e.g. saltasaurids and *Magyarosaurus*) indicates that body size cannot be a reliable indicator of track-gait. Thus, for the purposes of this study, it is here considered that taxonomy, rather than body size, is the better predictor of gait-type. It is difficult to assign sauropod trackways to their trackmaker more precisely than either narrow-gauge or wide-gauge types because of the very limited number of derived features in the fore and hind feet of distinct sauropod lineages that can be unambiguously recognised in trackways (though see Wilson 2005b). Provided trace fossils can be accurately assigned to particular taxa, analyses of separate body fossil and trace fossil datasets have the advantage that they yield two independent assessments of the environmental associations for the organisms concerned. Such an approach may reinforce the support for the hypothesis that a given clade made the trace fossil, or might reveal incongruence that would require reassessment of the putative trace fossil makers. If congruence between the body fossil and trace fossil signals exists, it is then perhaps justifiable to unite the datasets to produce a 'combined evidence' analysis of the environmental associations. Thus, trackways and body fossils have their own particular advantages and disadvantages for palaeoecological research and therefore both types of data are analysed separately and in combination.

One additional problem pertaining to trackways is that there may be differences within a single trackmaker across varying substrates (Bromley 1996; Allen 1997; Milàn 2006; Falkingham *et al*. 2009), e.g. across a boggy surface versus a flat arid terrain. Although it

is possible that differences in substrate account for differences in gait, this seems unlikely to extend to large variation such as that between narrow and wide-gauge tracks (Milàn 2006). This is further supported by the discovery of narrow and wide-gauge tracks alongside one another in a single heterogeneous environment (Day *et al*. 2002, 2004).

With regard to body fossils, there is a much wider choice of possible comparisons, such as neosauropods versus non-neosauropods, titanosaurians versus non-titanosaurians or diplodocoids versus macronarians. In this study, the majority of the analyses examine the environmental associations of titanosaurs versus non-titanosaurs. This enables the implementation of 'combined evidence' analyses in which narrow-gauge trackways and non-titanosaur body fossil data are combined and compared to wide-gauge trackways plus titanosaur body fossil data, providing two independent lines of evidence to test for environmental associations.

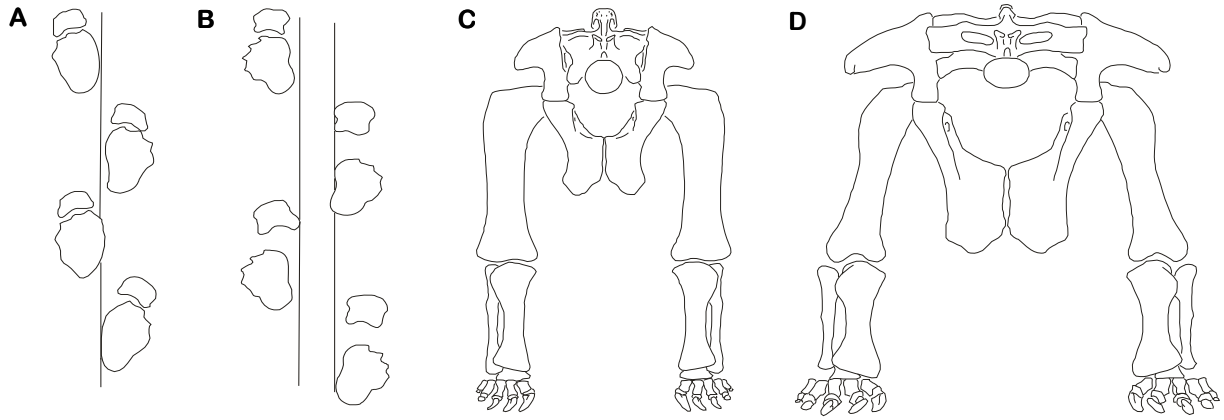

FIGURE 2.1. The two main sauropod track types: (A) "Narrow-gauge" trackway and (B) "Wide-gauge" trackway. Reconstructed pelvic girdles and hindlimbs, in anterior view, of: (C) the non-titanosaur *Camarasaurus* and (D) the titanosaur *Opisthocoelicaudia*. The vertical lines in A and B illustrate the distance separating left and right prints in the trackways. Images modified from Lockley *et al*. (1994) and Wilson and Carrano (1999).

Wilson and Carrano (1999) noted that basal titanosauriforms such as *Brachiosaurus* and *Euhelopus* have femoral morphologies that are intermediate between those in narrow-gauge non-titanosaurs and wide-gauge titanosaurs. Therefore the body fossil data are also analysed using a division into non-titanosauriforms and titanosauriforms, as well as a partition into non-titanosaurian titanosauriforms and titanosaurs to test for differences within Titanosauriformes.

Macronaria is a major sauropod clade that is largely composed of the Titanosauriformes and a few basal genera such as *Camarasaurus*. A recent study of Cretaceous dinosaurian distributions suggested that: 'Sauropods show little evidence for broad environmental associations: a significant negative association between Macronaria and coastal environments may be a result of taphonomic processes' (Butler *et al*. 2007: p. 54-55). Furthermore, Butler and Barrett (2008: table 1) also reported a statistically significant ($p < 1x10^{-4}$) positive association between Macronaria and inland environments. This possibility is tested by comparing macronarians with non-macronarians and through restriction of the current dataset to Cretaceous occurrences. In addition, Butler and Barrett's (2008) dataset is re-analysed to look for patterns at the taxonomic levels of titanosauriforms and titanosaurs.

Uneven sampling of environments through time

Trends in the diversity and abundance of taxa through time, combined with uneven sampling of depositional environments, could create an additional problem for palaeobiologists searching for environmental associations. For example, suppose the ratio of inland to coastal localities sampled from the Jurassic is 1:4 and from the Cretaceous is 4:1. Furthermore, suppose that titanosaurs were rare during the Jurassic and common during the Cretaceous relative to non-titanosaurs, so that the ratio of titanosaurs to non-titanosaur individuals is 1:10 in the Jurassic and 10:1 in the Cretaceous. Finally, suppose that titanosaurs and non-titanosaurs exhibited no

environmental preferences so that they were evenly distributed across the two environmental categories. Under this scenario, if 110 sauropod individuals were collected from the Jurassic, approximately ten of these would be titanosaurs and 100 would be non-titanosaurs. If these taxa display no environmental preferences, then it would be expected that eight titanosaurs and 80 non-titanosaurs would be from coastal localities and two titanosaurs and 20 non-titanosaurs from inland localities. If 110 sauropod individuals were then collected from the Cretaceous, we would expect 80 titanosaurs and eight non-titanosaurs from the inland localities, and 20 titanosaurs and two non-titanosaurs from the coastal localities. The total (Jurassic+Cretaceous) dataset would comprise 82 titanosaurs and 28 non-titanosaurs from inland localities, and 28 titanosaurs and 82 non-titanosaurs from coastal localities. This skewed distribution passes the chi-square test (see below), but the uneven distribution does not result from environmental preferences: the skew is a by-product of the combination of long-term trends in the relative abundances of the two taxon categories and two environmental categories.

There are grounds to believe that investigations of environmental associations in sauropods must deal with precisely the scenario outlined above. Our current understanding of sauropod diversity patterns is that non-titanosaurs were diverse during the Jurassic, declined in the Early Cretaceous and became extinct in the early Late Cretaceous, whereas titanosaurs were rare in the Jurassic but increased in diversity and abundance in the Cretaceous (Upchurch and Barrett 2005; see also Chapter 4). To investigate the possible effects of fluctuations of inland and coastal environments, the relative sampling rates of these two environments for sauropod-bearing localities have been calculated for each stage of the Jurassic and Cretaceous. However, to avoid the potential circular reasoning that arises from only considering sauropod-bearing localities (i.e. it is possible that there were as many coastal localities capable of preserving large-bodied terrestrial vertebrates during the Cretaceous as there were during the Jurassic, but fewer of them are recognised during the Cretaceous because data have only been

collected on sauropod-bearing localities and because titanosaurs preferred inland habitats), information on the numbers of ornithischian-bearing localities (www.pbdb.org; Carrano 2008b) have also used.

Table 2.3 shows that the percentage of coastal sauropod-bearing localities during the Jurassic is 19.4%, whereas during the Cretaceous this falls to 8.4%. For numbers of ornithischian-bearing localities, Table 2.3 shows that coastal environments contribute 23.2% of Jurassic and only 7.5% of Cretaceous localities. Given that several ornithischian clades apparently display a positive association with marine/coastal localities during the Cretaceous (Butler and Barrett 2008), the sauropod and ornithischian data taken together and separately (Table 2.3) suggest that coastal localities are indeed under-represented during the Cretaceous relative to the Jurassic. Thus, the possibility that statistically significant environmental associations relating to titanosaurs versus non-titanosaurs are an artefact of uneven sampling of inland and coastal habitats during the Jurassic and Cretaceous needs to be eliminated.

TABLE 2.3. The relative abundances of inland and coastal environments during the Late Triassic to Late Cretaceous, based on the numbers of localities producing sauropod body fossils, ornithischian body fossils, and combined sauropod and ornithischian body fossils.

Ma	**Geological stage**	**Sauropod body fossils + tracksites**		**Ornithischian body fossils + tracksites**	
		Inland localities	**Coastal localities**	**Inland localities**	**Coastal localities**
228	Carnian	3	0	2	2
216.5	Norian	5	0	2	0
203.6	Rhaetian	2	1	1	0
199.6	Hettangian	7	7	30	5

196.5	Sinemurian	10	4	28	1
189.6	Pliensbachian	7	3	5	1
183	Toarcian	8	3	5	0
175.6	Aalenian	8	1	1	1
171.6	Bajocian	15	2	2	1
167.7	Bathonian	21	10	1	1
164.7	Callovian	20	1	4	0
161.2	Oxfordian	24	3	11	1
155.7	Kimmeridgian	241	38	33	11
150.8	Tithonian	234	71	35	24
145.5	Berriasian	30	3	22	3
140.2	Valanginian	31	2	24	2
136.4	Hauterivian	44	4	35	3
130	Barremian	59	13	55	2
125	Aptian	101	8	97	7
112	Albian	140	28	196	31
99.6	Cenomanian	41	3	39	5
93.5	Turonian	53	1	16	1
89.3	Coniacian	46	1	12	1
85.8	Santonian	38	0	19	1
83.5	Campanian	84	4	268	9
70.6	Maastrichtian	118	5	117	3

Geological period	**Sauropods: % coastal relative to total**	**Ornithischians: % coastal relative to total**	**Sauropods + Ornithischians: % coastal relative to total**
Triassic	9.1%	28.6%	16.7%
Jurassic	19.4%	23.2%	20.2%

Cretaceous	8.4%	7.5%	7.6%

The effects of trends in the relative abundance and/or diversity of taxa and environments can be ameliorated by searching for environmental associations using narrower time bins. If titanosaurs and non-titanosaurs displayed genuine habitat preferences, then statistically robust environmental associations should persist even when the data are drawn from a narrower time window in which the relative abundance of inland and coastal environment types does not change markedly. Therefore, analyses are repeated using Cretaceous, Early-early Late Cretaceous (Berriasian-Coniacian) and stage level time-slices.

'Jack-knifing' the data

One danger with the current type of analysis is that the results may be dominated by short-lived windows of exceptional preservation that overwhelm signals in the rest of the dataset. This is a particular concern with the trackway data because 73 out of 190 localities (38.4%) are based on a mega-tracksite from the Early Cretaceous of the Republic of Korea (Lim *et al*. 1989; Lee *et al*. 2000; Lockley *et al*. 2006). Thus, the decision to treat this mega-tracksite as 73 separate localities, rather than one large locality, could make an important difference to the results. Therefore, the trackway data have been re-analysed after removal of all but one of the Korean tracksites (leaving 118 localities). However, the subsumation of 73 separate Korean tracksites into just one locality could be regarded as too severe. The description of these trackways indicates that at least six main tracksites can be distinguished from each other on the basis of spatial and stratigraphic separation, and so the analyses have also been run with Korean tracksites represented by these six regions (following the 'tracksite region' method of determining numbers of localities). Finally, the USA track record also comprises a large proportion of the tracksite dataset (17%), including a large number of Early Cretaceous coastal localities; thus, analyses have been run which exclude these tracksites.

Statistical tests

The rationale for investigating and testing environmental associations is as follows. If there are two environments (A and B) and two types of organism (X and Y), then the null hypothesis is that X and Y are distributed across A and B with no significant skew or bias. In ecological studies, this null hypothesis can be tested using a variety of statistical tests, with the G-test and Pearson's chi-square test the two most commonly used (Sokal and Rohlf 1987; Waite 2000; Hammer and Harper 2006). Both tests are used for determining the degree of difference between observed and expected values (i.e. the 'goodness of fit') for two sets of data when the null hypothesis to be tested is that there is no distributional bias or skew (Waite 2000; Hammer and Harper 2006). The two tests generally give the same results (Sokal and Rohlf 1987), but the G-test has the disadvantage of being impossible to calculate if some observed values are zero, because logarithms are used in its calculation (Waite 2000). Because many of the analyses include observed values of zero, Pearson's chi-square test is the more appropriate method for this study. The use of chi-square tests in palaeoenvironmental analyses also has precedents in fossil invertebrate studies (e.g. Peters and Bork 1999; Scholz and Hartman 2007; De Francesco and Hassam 2008) as well as the dinosaur analysis of Butler and Barrett (2008). In the context of palaeoecology, uneven sampling of fossils from different environments introduces a complicating factor. If three times as many fossils of group X have been collected from environment A relative to environment B, then a non-skewed distribution would be one in which three times as many members of group X (that were living in that environment at the time) are found in environment A compared to B. Therefore the relative sampling of each taxon type and environmental category must be taken into account when calculating the expected number of occurrences. Thus, the expected number of occurrences of taxon X (i.e. the expected number of fossils of X that should be found given a non-skewed distribution) in environment A (EXA) is given by:

$$EXA = NT \times [(NX/NT) \times (NA/NT)] \quad (1)$$

Where NX is the total number of occurrences of members of group X (in any environment), NA is the number of occurrences of environment A, and NT is the total number of environments (modified from Waite 2000: see also Butler and Barrett 2008). Equation (1) simplifies to:

$$EXA = (NX \times NA)/NT \quad (2)$$

The other three expected values required for the chi-square test are given by:

$$EXB = (NX \times NB)/NT \quad (3)$$

$$EYA = (NY \times NA)/NT \quad (4)$$

$$EYB = (NY \times NB)/NT \quad (5)$$

The formulae above were used to calculate the expected values in Chapter 3. For example, if X and Y are designated to represent narrow- and wide-gauge trackways respectively, and A and B to represent inland and coastal localities where such tracks are found, then EXA is the expected number of times that narrow-gauge trackways should occur in inland environments if there is no skew in the distribution.

Statistical significance is determined with reference to the chi-square distribution (Waite 2000). Usually a chi-square probability of 0.05 is used as the cut-off for accepting or rejecting the null hypothesis. However, in this study, the chi-square test has been applied 134 times in order to explore different aspects of the dataset. Given a *p*-value of 0.05 as the boundary between statistical significance and non-significance, one in 20 chi-square analyses would be expected to 'pass' even though the data were effectively random. There are several tests available for identifying which of these pairs of samples

are significantly different, with the two most common ones being Tukey's honestly significant difference and the Bonferroni test (Hammer and Harper 2006). However, the first of these tests has the disadvantage of reporting too high *p*-values when sample sizes are unequal (Hammer and Harper 2006), making it unsuitable for the current analyses. The Bonferroni test subjects the samples to pairwise comparisons, akin to the chi-square analyses, but uses much lower significance levels (Rice 1989), and is thus the more appropriate method here. This correction states that the *p*-value for determining statistical significance is given by α/n, where α is the original desired *p*-value (in this case 0.05) and n is the number of analyses (=134). Thus, the *p*-value used to determine statistical significance is 3.73×10^{-4}. By lowering the significance level, the Bonferroni correction greatly reduces the likelihood of incorrectly attributing significance to the pairwise comparisons (Waite 2000). A second advantage of the Bonferroni correction is that it can be used when the multiple analyses are independent or non-independent from each other, as is the case for the current study.

One additional point is that the formula used above informs us of the environmental preferences of each group in relation to one another; for example, titanosaurs preferred inland environments in comparison to non-titanosaurs. However, this result does not necessarily mean that titanosaurs preferred inland more than coastal environments, but only that they showed a greater preference for inland environments than non-titanosaurs. This is a subtle difference, but the above inland titanosaur preference could result from three different patterns: (1) Titanosaurs prefer inland environments but non-titanosaurs show no preference; (2) Titanosaurs show no preference but non-titanosaurs prefer coastal environments; or (3) Titanosaurs prefer inland environments *and* non-titanosaurs prefer coastal environments. To tease this apart, chi-square tests were also applied to each separate group to test the null hypothesis that each group is evenly distributed over both environments.

Diversity

Taxic and phylogenetic diversity estimates

Introduction

There are two main methods for measuring diversity. First, the 'taxic' approach (Levinton 1988) defines the total geological range of each taxon and sums the numbers of taxa present in each time interval to produce a diversity curve. This approach has the benefits of: (1) allowing all taxa to be incorporated, (2) being computationally simple to implement and (3) not requiring knowledge of detailed phylogenetic relationships. However, the taxic method has been strongly criticised for its reliance on what is often considered an incomplete and biased fossil record, and led to the development of a second method, the phylogenetic approach (Novacek and Norell 1982; Norell and Novacek 1992a, b; Smith 1994). This method calibrates the phylogenetic relationships between taxa against stratigraphy. This extrapolation identifies 'ghost' ranges: these are lineages that represent the inferred presence of a taxon over a particular temporal interval, whose existence is predicted by phylogeny, but for which there is no direct fossil evidence (Norell 1992a, 1993). Phylogenetic diversity estimates take information on the observed temporal ranges of lineages within a cladogram and incorporate additional diversity data inferred from these 'ghost' ranges, thereby partially correcting for gaps in the fossil record. There are several criticisms of the phylogenetic method, however. For example, by only correcting for the first appearance times of taxa (i.e. through 'ghost' lineages), the phylogenetic method introduces an asymmetrical bias by not also extending extinction times forwards (Wagner 1995, 2000a; Foote 1996). Additionally, the assumption that ancestral taxa are rarely found in the fossil record (Lane *et al*. 2005) means that they are absent among the terminal taxa of a phylogeny (Benton and Storrs 1994). Also, when misdiagnosed ancestors are included in

phylogenies, the addition of ghost lineages may over-inflate diversity estimates (Lane *et al*. 2005).

The use of the taxic approach has not been abandoned, however; many workers have utilised enhanced statistical techniques in attempts to resolve its problems (e.g. Alroy *et al*. 2008). Thus, both the taxic and phylogenetic methods have been applied here; through this pluralistic approach the disadvantages of both methods can hopefully be overcome (Wagner 1995; Foote 1996; Lane *et al*. 2005).

Fit of sauropodomorph phylogenies to stratigraphy

Before phylogenies are used to reconstruct diversity, some idea of how well they fit stratigraphy is needed in order to see how closely they sample and reflect the fossil record. Phylogenies are generally obtained solely from biological data and are usually independent of temporal information (Norell 1996). Thus, by mapping cladograms onto stratigraphic range charts two independent methods for understanding the evolution of a group of organisms can be combined (see Pol and Norell 2006, and references therein). Numerous measures have been proposed for comparing the stratigraphic fit to a phylogeny (e.g. Norell and Novacek 1992a; Benton and Hitchin 1997; Siddall 1998; Wills 1999; Pol *et al*. 2004; Wills *et al*. 2008) and can also be used to compare competing phylogenies. Most dinosaur datasets have been demonstrated to show extremely high congruence between phylogeny and stratigraphy (Brochu and Norell 2000; Wilson 2002; Rauhut 2003; Pol and Norell 2006; Wills *et al*. 2008), leading Wills *et al*. (2008) to comment that our knowledge of the dinosaur fossil record is more than adequate for investigating temporal patterns of dinosaur diversity. Wills *et al*. (2008) found that both the sauropod phylogenies of Wilson (2002) and Upchurch *et al*. (2004a) showed excellent stratigraphic congruence (using several variations of the 'Gap Excess Ratio'), though the former performed slightly better. For basal sauropodomorphs, Wills *et al*. (2008) found that the phylogeny of Upchurch *et al*. (2007a) showed much greater

stratigraphic congruence than that of Yates (2007), though both were out-performed by the sauropod phylogenies. However, it is possible that this poorer performance of basal sauropodomorph phylogenies also reflects the shorter amount of time (Late Triassic–Early Jurassic) under investigation in comparison to the sauropod phylogenies (Early Jurassic–Late Cretaceous), thereby potentially increasing the impact of stratigraphic uncertainties. Regions of diversity curves where different phylogenies produce comparable results may represent better-constrained time periods, whereas incompatible areas may represent more poorly understood portions of Sauropodomorpha (either in terms of missing lineages, low-resolution dating and/or a poor rock record, or differing interpretations of the same material; Benton 2001; Wills 2002; Smith and McGowan 2007); consequently, a number of independent phylogenies have been utilised. Diversity has been plotted against the geological timescale of Gradstein *et al*. (2005), with origins and stratigraphic ranges dated to substage level (see 'Geological age of taxa' below).

Two non-parametric statistical methods have been applied to assess the degree of correlation between each of the diversity curves: Spearman's rank correlation coefficient is a non-parametric method which compares the order of appearance of data points on two axes (Hammer and Harper 2006). Kendall's tau rank correlation coefficient is another non-parametric method but differs in that it assesses whether the curves from two datasets are in phase with another (Hammer and Harper 2006). These have been calculated with PAST (Hammer *et al*. 2001). Computational details of both tests are provided in Press *et al*. (1992).

Taxonomic units of analysis

Several authors have highlighted problems with using the unit of species for estimating diversity (e.g. Smith 2001), noting that it 'results in one of the worst correlations with underlying lineage diversity' when sampling is poor (Robeck *et al*. 2000, p. 186). In the

present dataset, however, the distinction between genus and species is often unclear; the majority of sauropodomorph genera are monospecific (94%) and thus there can be little difference between species and genus level diversity curves (Upchurch and Barrett 2005). Indeed, genus and species diversity curves are strongly correlated for sauropodomorphs (P. Barrett pers. comm. 2009). Moreover, most large analyses of sauropodomorph phylogeny (except Lloyd *et al*. 2008) have been conducted at the genus level, making them broadly comparable. Higher taxic levels (e.g. families) have been demonstrated to be unsuitable proxies for genera in macroevolutionary studies (e.g. Rhodes and Thayer 1991; Smith 1994; Barrett and Upchurch 2005; Tarver *et al*. 2007) and were not examined here. Analyses have thus been implemented at the generic level: because it was conducted at the specific level, the supertree of Lloyd *et al*. (2008) will be the exception. In this supertree, a number of species belonging to individual genera were recovered as paraphyletic (e.g. *Haplocanthosaurus* and *Brachiosaurus*); therefore each species included in the supertree will be considered a unique taxon for the purposes of this study. For phylogenetic diversity curves, the taxa used are restricted to those genera incorporated into the original analyses; however, the taxic diversity curve incorporates all valid sauropodomorph taxa (see Table 2.2).

Geological age of taxa

One of the most serious issues with constructing diversity curves is that the geological ages of taxa often cannot be constrained with precision. Few fossil taxa can be directly dated (e.g. by radiometric dating), and even when they can the dates obtained are usually restricted to the horizons above and/or below the fossil-bearing layer. Most vertebrate fossils are dated using indirect methods, such as biostratigraphy, which tend to be limited in resolution to the stage level (e.g. Campanian), or even coarser time bins, and can impose some circularity depending on the taxa involved. For the Mesozoic, stage intervals vary in temporal range from ca. 3-13 Myr in duration (Gradstein *et al*. 2005); thus, any fossil indirectly dated will have an associated error in its temporal

range. Many sauropodomorph fossils cannot be dated more accurately than to the epoch level (e.g. Middle Jurassic), with an animal dated as Early Cretaceous confined only to a 46 Myr period. For example, estimates for the age of the Chinese somphospondyl *Euhelopus* span a 39 Myr interval from the Tithonian through to the Aptian (Wilson and Upchurch 2009).

As long as error is randomly distributed, it can only degrade a genuine signal: it cannot create an artificial one (Raup 1991; Smith 2001). Previous workers (e.g. Sepkoski 1993; Adrain and Westrop 2000) have demonstrated that stratigraphical and taxonomic revisions have had little significant effect on overall diversity patterns. Thus, although the most recent literature has been used as the basis for the stratigraphic ranges and taxonomy, the overall observed diversity curve is not expected to differ greatly from those of previous studies. In most instances the full suggested temporal span of a taxon has been used, although in some cases estimates based on more accurate dating techniques have been utilised (see Table 2.2). This is the most conservative method for providing ages for each sauropodomorph occurrence, although it obviously introduces errors into the analysis, in particular the phylogenetic diversity estimates. An alternative method might be to choose the most probable age rather than a range; such an approach might work for some taxa (e.g. *Bellusaurus* is probably from the latest Middle Jurassic), but would be impossible for other occurrences (e.g. there is no indication as to which part of the Early Cretaceous many Chinese specimens came from). As such, this method would introduce an asymmetrical bias to the analyses. However, it is not only the taxonomic data that are treated in this conservative way. The dating of formations and collections are also based on the full possible stratigraphic range; thus, the corrections for sampling (see below) use datasets that are based on the same geological ages as the taxonomic data. Consequently, any errors in dating are spread equally between the biological and geological data and should not have a notable impact on overall ‘corrected’ diversity.

Preservational biases and sampling quality

Taphonomic and sampling biases have the potential to greatly affect attempts to determine generic richness, and thus construct diversity curves, for fossil taxa (e.g. Behrensmeyer *et al*. 2000; Miller 2000; Alroy *et al*. 2001, 2008; Upchurch and Barrett 2005; Smith 2007; Smith and McGowan 2007; Uhen and Pyenson 2007; Peters 2008; Barrett *et al*. 2009; Butler *et al*. 2009c; Wall *et al*. 2009). Following the work of Raup (1972), numerous workers have demonstrated that both the amount of rock outcrop and the environments preserved therein have varied throughout geological time. For example, the ratio of terrestrial to marine environments at any time interval is dependent upon sea level (Smith and McGowan 2007). As a consequence of this, diversity could merely mirror the volume of rock outcrop as well as the number of opportunities to observe fossils (NOOs: Raup 1972, 1976; Alroy *et al*. 2001; Peters and Foote 2001, 2002; Smith 2001; Smith *et al*. 2001; Crampton *et al*. 2003; Peters 2005, 2008; Smith and McGowan 2005, 2007; Upchurch and Barrett 2005; Uhen and Pyenson 2007; McGowan and Smith 2008; Barrett *et al*. 2009; Butler *et al*. 2009c; Marx 2009). Thus, apparent diversity cannot be entirely controlled by rock outcrop or the NOOs if it is to reflect genuine evolutionary patterns. Therefore, a range of sampling proxies has been considered in comparisons with sauropodomorph diversity, in an attempt to tease apart any genuine biological signal from that of the rock record.

Rock outcrop

Upchurch and Barrett (2005) and Barrett *et al*. (2009) utilised DBFs as a proxy for rock outcrop (based on data from Weishampel *et al*. 2004a), plotting the number of DBFs through time. These authors chose to use DBFs rather than sauropodomorph-bearing formations (as utilised by Hunt *et al*. 1994) because if a rock unit is capable of preserving large terrestrial vertebrates (i.e. any dinosaur) then it should also be capable of preserving sauropodomorphs; i.e. rock units lacking (or with low diversities of)

sauropodomorphs, but preserving other dinosaurs, may reflect genuine situations where sauropodomorph diversity was depauperate. Thus, DBFs have been used for the updated diversity analyses.

A more refined version of using DBFs is to quantify the rock record itself. Peters and Foote (2001) estimated the amount of marine sedimentary rock outcrop at epoch level for the Phanerozoic of the USA and noted that fluctuations are positively correlated with generic marine diversity. Similarly, Smith and McGowan (2007) calculated outcrop area of marine and terrestrial sediments at stage level for the Phanerozoic of western Europe. They found that the size and timing of two of the five major Phanerozoic mass extinctions are strongly predicted by rock outcrop but concluded that overall diversity trends (as well as the K/P extinction event) were not the result of rock area bias. McGowan and Smith (2008) also highlighted the likelihood of the global Phanerozoic diversity curve being disproportionately influenced by European and North American fossil data. However, Wall *et al*. (2009) recovered a strong correlation between Phanerozoic marine diversity and global rock outcrop, albeit through implementing a much coarser global estimate and using epoch level time bins.

For the purposes of this study, the terrestrial and marine rock record data of Smith and McGowan (2007) were utilised to construct Mesozoic rock outcrop curves. These were then compared with the diversity curves produced for Sauropodomorpha (TDE and PDE), as well as alongside the taxic diversity from western Europe alone (TDE_{WE}) in an attempt to clarify whether this region might be a suitable proxy for the global rock record (at least for sauropodomorphs).

Collecting effort

As well as geological biases (see above), additional human biases exist in terms of taxonomic artefacts (Uhen and Pyenson 2007; Alroy *et al*. 2008; Peters 2008) and the

disproportionate sampling and study of different time intervals (e.g. the Campanian–Maastrichtian has received considerably more attention than most other Mesozoic stages).

In addition to utilising DBFs and rock outcrop, diversity has been compared with dinosaur-bearing collections (DBCs), derived from *The Paleobiology Database* (www.pbdb.org; Carrano 2008b). These collections represent discrete, independent samples of dinosaurs from specific geographic and stratigraphic localities; they have been as finely resolved as the published record allows. Similar collection-based methods have been used by previous authors in attempts to investigate the diversity of numerous groups (e.g. Crampton *et al*. 2003; Uhen and Pyenson 2007; Alroy *et al*. 2008; Carrano 2008a).

An additional way to assess collecting effort is to construct collector curves for fossil taxa by plotting the cumulative number of newly described taxa against the date of description. When the rate of new discoveries declines markedly, it is assumed that true diversity (at least in terms of those taxa that were fossilised and thus had a chance of being discovered) has been approached (Benton 1998). The near-complete collector curve should thus have a sigmoid curve with a slow initial rise followed by a phase of rapid increase, before levelling off towards an asymptote (Benton 1998, 2008b). Another method is to look for correlations between the geological ages of taxa and their years of description. If we were increasingly driving back (or forward) the age of the oldest (or youngest) taxon, then we might suspect that there were large gaps in sampling (Benton 1998; Fountaine *et al*. 2005). If, at the other end of the spectrum, the fossil record was extremely well-sampled then we might expect new discoveries to be from geological ages from which we already have numerous taxa. A more likely scenario is that new discoveries from an overall well-sampled fossil record will fill in the various internal stratigraphic gaps within that record. Here both of these measures have been utilised to further assess the contribution of human error in estimating diversity.

Residuals

The effect of sampling biases on diversity can also be analysed by constructing a model in which sampling opportunity perfectly predicts the TDE, then subtracting this from the TDE, leaving a residual 'unexplained diversity signal' (Smith and McGowan 2007; Barrett *et al*. 2009; Butler *et al*. 2009c). These models have been constructed by independently sorting $_{log}$ sampling bias (e.g. DBFs and DBCs) and $_{log}$ TDE from low to high values, then fitting a linear model of the form y = mx + c to the ordered data, where x is the sampling proxy datum, m is the gradient of the line and c is a constant.

This equation was applied to the sampling bias data in its original order (i.e. plotted against geological time) to derive a temporal series of modelled (or predicted) diversity (MDE). Lastly, MDE was subtracted from TDE to obtain the residual, which therefore represents fluctuations in diversity that cannot be explained in terms of the sampling bias (Smith and McGowan 2007; Barrett *et al*. 2009; Butler *et al*. 2009c). This last step was then repeated, replacing TDE with PDE (Barrett *et al*. 2009), to obtain residuals of PDE from MDE. Using this residuals-based method, TDE and PDE were then compared with the sampling biases outlined in the preceding sections. Time periods in which residuals vary between different sampling biases could help in identifying which factors affect particular temporal intervals.

Rarefaction

One of the fundamental problems with diversity analyses is their dependence on sample size (Sanders 1968; Raup 1975; Colwell and Coddington 1994). Many early attempts to analyse diversity (e.g. Hairston and Byers 1954) found that their results depended on the size of the total sample, with diversity increasing with sample size. This is because not all species will be equally abundant; thus, rare species are less likely to be found unless there is a large sample size (Hammer and Harper 2006). To overcome this

problem, Sanders (1968) developed the method of rarefaction (later corrected, built upon and discussed further by: Hurlbert 1971; Simberloff 1972; Heck *et al*. 1975; Raup 1975; Tipper 1979; Gotelli and Colwell 2001; Hammer and Harper 2006) to compare taxonomic richness in samples of different sizes and to investigate the effect that sample size has upon taxon counts (Hammer and Harper 2006). This method uses the number of specimens of taxa expected in a sample if the sample had the same size as that of the smallest sample in the dataset, i.e. all samples are rarefied to reduce and standardise them to the smallest sample size (Hammer and Harper 2006). For example, if we had two samples, one with 100 specimens and one with 20 specimens, we would standardise the larger sample to see what taxic count we would expect if we had only collected 20 of these specimens. As a consequence of the random nature of this selection of 20 specimens, this procedure should be repeated a number of times to converge on a range of expected values (Hammer and Harper 2006).

There are two main methods of rarefaction: individual-based and sample-based (see Gotelli and Colwell 2001). The former method standardises by the number of individuals; i.e. it provides the expected numbers of genera with increasing numbers of individuals sampled, assuming a random sample of individuals in the community (Gotelli and Colwell 2001). The second method of rarefaction computes taxic richness accumulation curves as a function of the number of samples (Gotelli and Colwell 2001; Hammer and Harper 2006). Individual-based rarefaction curves require absolute abundance data for each taxon (in terms of the number of individuals), whereas only presence-absence data is needed to calculate sample-based rarefaction curves (Gotelli and Colwell 2001). As only new genera increment the sample-based rarefaction curve, the targeting of only new genera (rather than finding new specimens of existing genera) does not introduces a bias (Colwell and Coddington 1994). Tipper (1979) listed four requirements of the rarefaction method: (1) collections to be compared should be taxonomically similar; (2) collections to be compared should have been obtained by using standardised sampling; (3) collections to be compared should be from similar

habitats; (4) rarefaction must be restricted to interpolation and not extrapolation of the number of individuals. The first and last of these four criteria are non-problematic: only sauropodomorphs are being considered and also only at the generic level (or specimens that must represent different distinct genera), and the data are not being extrapolated. Criteria two and three are more complicated though. Although criterion 2 is problematic for both methods of rarefaction, it is less of an issue for sample-based rarefaction as this approach accounts for patchiness in the data that result from sample heterogeneity (Colwell *et al*. 2004), whereas individual-based rarefaction overestimates the number of taxa that would have been found with less effort (Gotelli and Colwell 2001; Ugland *et al*. 2003). Sample-based rarefaction curves are plotted from samples taken randomly; they take into account the number of taxa and their identity, but information on the distribution of individuals among taxa is not utilised in their calculation (Gotelli and Colwell 2001). Furthermore, Westrop and Adrain (2001) demonstrated that the same overall diversity patterns were recovered when analysing data collected from two sources which had not been obtained through standardised sampling, i.e. the published literature and from field collections. Westrop and Adrain's (2001) study, along with the above mentioned benefit of sample-based rarefaction (Gotelli and Colwell 2001; Colwell *et al*. 2004), indicates that the problem of using standardised sampling might be at least partly ameliorated. Criterion 3 is probably the most problematic of Tipper's (1979) requirements. Individual-based rarefaction is appropriate for comparisons of alpha diversity at individual sites, but is not suitable for comparisons of diversity across spatial or environmental gradients (Waite 2000; Hammer and Harper 2006). However, sample-based rarefaction has been shown to be suited to examining diversity across environments (e.g. Rosenzweig 1995; Ugland et al. 2003; Crist and Veech 2006, and references therein) and the benefits outlined above (i.e. accounting for data patchiness resulting from sample heterogeneity) also support its usage in this manner.

Rarefaction has been used to address a wide range of problems in paleobiology, including: the effects of sample size on diversity (Miller and Foote 1996; Nehm 2001;

Jamniczky *et al*. 2003; Benton *et al*. 2004; Bush *et al*. 2004); estimates of taxonomic richness (Aguirre *et al*. 2000; Watkins 2000; Alroy *et al*. 2001; Barnosky 2001; Fastovsky *et al*. 2004; Peters 2006; Kroh 2007) and abundance (Bulinski 2007; Davis and Pyenson 2007; Olszewski and Kidwell 2007); morphological variety (Foote 1992); comparisons of diversity between biofacies and sea-level changes (Stanton and Evans 1972; Westrop and Adrain 1998; Amati and Westrop 2006; Scarponi and Kowalewski 2007), and fluctuations in diversity at extinction and radiation events (Adrain *et al*. 2000; Jaramillo 2002; Shen and Shi 2002; Hammer 2003; Fan and Chen 2007; Berglund *et al*. 2008; Ruta and Benton 2008; Kriwet *et al*. 2009).

Nearly all analyses of dinosaur diversity have been limited to counts of numbers of taxa or lineages per stage. Thus far, only one published study has implemented rarefaction in an attempt to elucidate global dinosaur diversity: Fastovsky *et al*. (2004) utilised the global dinosaur locality dataset of Weishampel *et al*. (2004a), pruning it to exclude generically indeterminate material. These authors demonstrated a steady increase in diversity throughout the Mesozoic and argued that dinosaurs were not in decline in the last 10 Myr of the Mesozoic. This study has been criticised by several workers (Archibald 2005; MacLeod and Archibald 2005; Sullivan 2006), who questioned the interpretation of the rarefied data by Fastovsky *et al*. (2004) and suggested (after re-analysis) that a Maastrichtian decline in dinosaur diversity is still well supported (Barrett *et al*. [2009] also recovered support for this decline). However, Carrano (2008a) demonstrated that dinosaur diversity for the latest Cretaceous of North America shows much less variation between formations and time intervals than is documented by stage level diversity counts and suggested that, rather than reflecting an end-Cretaceous decline, Campanian–Maastrichtian fluctuations (at least for North America) are the product of ecological, environmental and sampling biases (particularly of an anthropogenic nature).

Following Fastovsky *et al*. (2004), all generically indeterminate occurrences were omitted from the global sauropodomorph database. Generic occurrences were then

split into their respective stratigraphic stages, with each taxon counted as present for each interval in which it occurred. Smaller time bins (i.e. substage) were not used because of constraints on minimum sample sizes for effective rarefaction (Krebs, 1999; Hammer and Harper 2006). Sample-based rarefaction (using the number of localities each genus is found at in each stage) was implemented in PAST (Hammer *et al*. 2001), with only time bins (7) containing 30+ samples rarefied. Following this, curves of rarefied diversity were constructed.

One potential problem with this method of rarefaction is the omission of generically indeterminate occurrences. Previous rarefaction analyses have excluded these and have only included numbers of occurrences of genera. However, in a given sample, it is unlikely that all individuals will be recognised to the level of genus: many sauropodomorph individuals cannot be recognised beyond clade or family level (e.g. Titanosauria). As such, a modified version of the rarefaction analysis is also implemented. For each locality, an additional genus is included for material representing any clade that cannot include any of the named genera. For example, if a site contains remains of *Dicraeosaurus*, as well as indeterminate diplodocid and diplodocoid elements, then its total generic diversity would be two because the indeterminate diplodocid materials cannot be referred to *Dicraeosaurus* (a dicraeosaurid diplodocoid; see Chapter 1) and must belong to a second taxon. However, the indeterminate diplodocoid could represent undiagnostic materials of either form and is thus not counted. The same procedure is applied when only indeterminate materials are present (i.e. two genera are considered present in a quarry that preserves indeterminate dicraeosaurid, diplodocid and diplodocoid materials). These indeterminate occurrences are summed and considered additional genera for each time bin. As well as enabling the inclusion of indeterminate materials and thereby attempting to assess 'cryptic' diversity, this method also has the advantage of greatly increasing the sample size for each time bin, which has obvious benefits for rarefaction (i.e. increasing the size of the smallest sample). Sample-based rarefaction, using 'all occurrences', has been implemented at

several different minimum sample sizes: 30 (22 stages included), 50 (18 stages), 70 (11 stages) and 90 (7 stages).

Comparisons with sea level

Closely related to the rock record is the record of fluctuating sea levels (Haq *et al*. 1987). It has long been noted that eustatic Phanerozoic sea level fluctuations coincide with many episodes of variation in marine diversity (Newell 1952; Johnson 1974; Hallam 1989; Smith 2001). Other workers have also observed a close correlation between patterns of sauropodomorph (and/or dinosaur) diversity and sea level fluctuations (Haubold 1990; Hunt *et al*. 1994; Upchurch and Barrett 2005). Although sauropodomorphs were terrestrial, sea level could have affected their apparent diversity abiotically, e.g. through controlling their preservation potential (Upchurch and Barrett 2005). The remains of terrestrial organisms may be more likely to reach aquatic environments during periods of high sea level, meaning they are more likely to be preserved (Haubold 1990). Another possibility is that available land area on which to preserve a terrestrial record will be greatly reduced during times of high sea level, resulting in a poorer fossil record (Markwick 1998).

Other authors have evoked biotic factors in an attempt to explain this correlation: i.e. allopatric speciation is likely to happen during high sea levels as land areas become separated, while during low sea levels there may be mixing of previously isolated organisms, potentially resulting in extinctions (Bakker 1977; Horner 1983; Weishampel and Horner 1987). Conversely, the formation of geographic barriers may also result in extinction events as the sizes of some habitats dwindle (Dodson 1990; Upchurch and Barrett 2005).

Four of the five diversity peaks (Bajocian, Kimmeridgian, Valanginian-Barremian, and Campanian-Maastrichtian) identified by Haubold (1990) and Hunt *et al*. (1994) as

correlating with high sea level were observed in the PDE of Upchurch and Barrett (2005), and two of the four diversity troughs correlated with low sea level (Oxfordian and Turonian-Coniacian). This suggests that these six intervals, at least, may potentially represent genuine (i.e. biotic) diversity signals rather than purely the effects of taphonomic biases.

This study has repeated earlier analyses by comparing 'corrected' sauropodomorph diversity (i.e. PDE, residuals and rarefaction) with the sea level curve of Haq *et al*. (1987). In addition, a finer-scale study has been implemented to look for correlations solely during the Late Cretaceous, utilising a recent backstripped sea level curve (Miller *et al*. 2005), which represents the global sea level record for the past 100 Myr. For both sea level curves, average sea level was calculated for each substage time bin. It should be noted, though, that the stratigraphy of Haq *et al*. (1987) differs considerably from the recent Gradstein *et al*. (2005) timescale. For example, the Oxfordian is dated as 145-152 Ma in the former and 155.7-161.2 Ma in the latter, while the Jurassic/Cretaceous boundary is dated at 131 Ma in the Haq *et al*. (1987) study but is now dated at 145.5 Ma (Gradstein *et al*. 2005). Thus, the re-calibrated Mesozoic sea level data of Haq *et al*. (1987) (as listed in Miller *et al*. [2005]) has been used.

Completeness metrics

New metrics

Sauropodomorph specimen completeness has been estimated by applying three variants of two different approaches, giving six completeness metrics in total. The first method (here termed the 'Skeletal Completeness Metric' [SCM]) is based upon dividing the skeleton up into different regions and then assigning percentages based on approximations as to how much of the skeleton is represented. Figure 2.2 and Table 2.4 shows how the skeleton has been partitioned and assigned percentages. Within these body regions, individual elements are also weighted: for example, a complete femur and a complete pes are each scored as 2% while a complete tibia is scored as 1%, reflecting the latter's smaller size and fewer elements in comparison with the femur and pes respectively. Absence of an element would result in a score of zero, while a tibia missing its distal half, for example, would be scored as 0.5%. Vertebral numbers vary across Sauropodomorpha (e.g. the number of cervical vertebrae varies from ten in the basal form *Plateosaurus*, to 12 in the macronarian *Camarasaurus*, 15-16 in diplodocids, and 17 in *Euhelopus* and mamenchisaurids; Wilson 2002; Galton and Upchurch 2004; Upchurch *et al*. 2004a) and so to determine the completeness of the neck, for example, the 15% value (see Table 2.4) has been divided by the total number of vertebrae that should have been present in life and then multiplied by the actual number preserved. Where a complete vertebral sequence is unknown for a taxon, this total number is inferred from comparisons with closely related taxa. Total percentages are always rounded to the nearest percentage point and the minimum level of completeness of an individual is 1% (i.e. an isolated phalanx still indicates the presence of an individual which should be registered by a completeness metric). Although these values are only approximations of the amount of skeleton represented, minor changes in the selected weightings should not have a marked affect on comparisons of overall completeness between specimens.

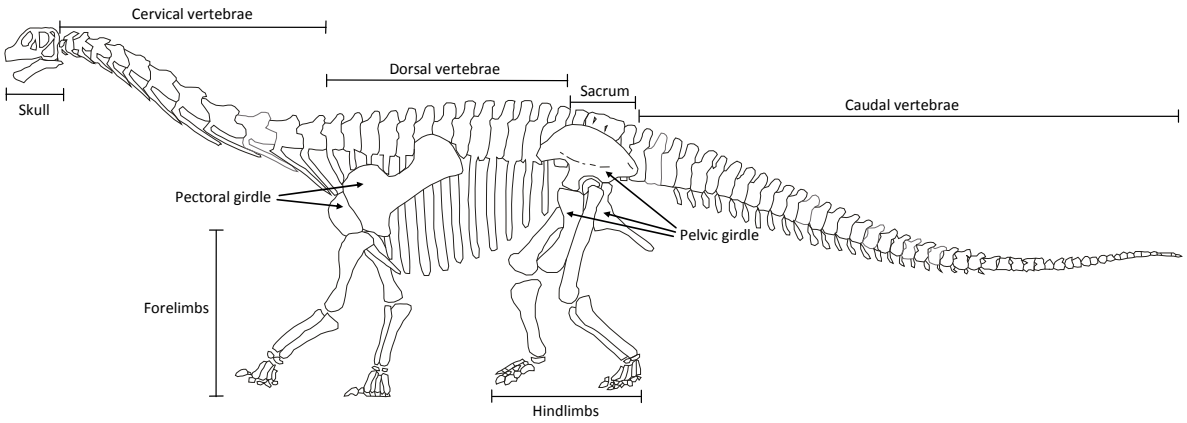

FIGURE 2.2. Skeletal outline of *Camarasaurus* (modified from Wilson and Sereno 1998), showing the body regions used to partition the skeleton (see Table 2.4 for further details).

TABLE 2.4. Percentages attributed to regions of the body based on the Skeletal Completeness (SCM) and Character Completeness (CCM) methods. Percentages are rounded to the nearest whole percentage point. See text for details.

Skeletal region	SCM	CCM
Skull	10	33
Cervical vertebrae and ribs	15	7
Dorsal vertebrae and ribs	15	9
Sacral vertebrae and ribs	5	2
Caudal vertebrae and ribs	20	8
Pectoral girdle	5	3
Forelimbs	12	10
Pelvic girdle	6	8
Hindlimbs	12	18
Miscellaneous	0	2

'Skeletal Completeness Metric 1' (SCM1) is the completeness (expressed as a percentage) of the most complete specimen known for that taxon. For example, *Apatosaurus* is known from dozens of skeletons (Upchurch *et al*. 2004b) but the most completely known individual (CM 3018) has an SCM1 score of 77%. SCM1 can be obtained for 88% of known sauropodomorph genera. The remaining 12% of taxa are more problematic because, despite a large amount of material, there are uncertainties regarding the associations of elements. For example, *Barapasaurus*, *Bellusaurus*, *Thecodontosaurus* and *Kotasaurus* are known from bonebed accumulations where the minimum number of individuals can be recognised, but not which elements belong to which individual (Upchurch *et al*. 2004a, and references therein; see also Rauhut and Lopez-Arbarello [2008] who noted that the *Kotasaurus* material is a chimera, including at least one additional sauropod taxon). Similarly, *Lapparentosaurus* is described as consisting of five individuals from five locations, but information regarding particular associations is not available (Ogier 1975; Bonaparte 1986; Mannion 2010). Such taxa have been omitted from the SCM1 analyses.

'Skeletal Completeness Metric 2' (SCM2) quantifies how much of the skeleton is known for a given taxon as a whole; that is, it utilises all known individuals of that taxon. For example, the Chinese taxon *Euhelopus* is known from two individuals that overlap, anatomically, in the middle trunk region (Wiman 1929; Wilson and Upchurch 2009). These two individuals (examplars a and b) have SCM scores of 37% and 27% respectively. Under SCM1, *Euhelopus* therefore has a score of 37%, but under SCM2 the two specimens are considered together, giving a score of 57%. Similarly, there are no entirely complete skeletons of the well-known taxa *Omeisaurus*, *Mamenchisaurus* and *Diplodocus*, but by using this second metric each of these can be demonstrated to be almost 100% complete in terms of osteological representation. SCM2 enables a more meaningful assessment of the completeness (of our anatomical knowledge) of taxa such as *Lapparentosaurus* and bonebed occurrences, e.g. *Bellusaurus* (see above). However, it is important to note that this benefit of SCM2 is also a potential weakness, as

incorrect scores are more probable because they rely more heavily on beliefs about the association of elements or the taxonomic affinities of individuals. The only taxon for which an SCM2 score has not been calculated is *Atlasaurus*, because of a lack of information in the original description (Monbaron *et al*. 1999). Although SCM2 and CCM2 have an advantage over SCM1 and CCM1 in that they include information from many individuals, thereby allowing taxa such as bonebed-based forms to be included (see 'Materials and Methods'). However, this strength of SCM2 and CCM2 is also a potential weakness: incorrect scores are more probable with these metrics because they rely more heavily on beliefs about the association of elements or the taxonomic affinities of individuals.

The second method, the 'Character Completeness Metric' (CCM), follows the same logic as SCM1 and 2, but the percentages assigned to different parts of the skeleton are based on their phylogenetic character richness. These weightings are based on calculating the average percentage of characters attributed to each region of the body in four independent sauropodomorph phylogenies (Wilson 2002; Upchurch *et al*. 2004a, 2007a; Yates 2007; see Table 2.5). Regions of the body have been separated in the same way as for the SCM (see Table 2.4), although an additional section has been required to accommodate characters that consider more than one region of the skeleton (for example, characters that relate to presacral vertebrae or to ratios between fore and hindlimbs). Of particular note is the much higher percentage attributed to the skull by the CCM than the SCM (33% versus 10%; see Table 2.4). As in the SCM, the CCM can be used to assign the percentage completeness contributed by an individual skeletal element, and it is immediately apparent that some elements have been considered more phylogenetically informative than others in these four sauropodomorph phylogenies. For example, a single, complete posterior dorsal vertebra can, on average, be scored for 7% of all characters, while a fibula can only be scored for 1%. Variants of the CCM, directly comparable to SCM1 and SCM2, are proposed, which are herein

referred to as 'Character Completeness Metric 1' (CCM1) and 'Character Completeness Metric 2' (CCM2). Thus, CCM1 gives the phylogenetic completeness of the best preserved individual belonging to a given taxon, whereas CCM2 gives the estimated phylogenetic completeness when anatomical knowledge is based on the sum of all individuals within that taxon.

In order to provide comparable analyses to those produced by Benton (2008a, b), the SCM and CCM scores of the type specimen of each sauropodomorph taxon have also been calculated (SCM_{ts} and CCM_{ts}). In cases where an author has selected a particular element from an individual to stand as the holotypic specimen, the SCM_{ts} and CCM_{ts} are calculated based on the entire individual, not just the holotypic specimen (as was also implemented by Benton 2008a, b). Where an individual cannot be determined among the type material (e.g. within a disarticulated bonebed with more than one individual), this taxon has been omitted. In total, 89% of taxa have been included in the SCM_{ts} and CCM_{ts} analyses. All of these metrics are relative to the theoretical maximum for a complete skeleton, i.e. the remains of all taxa could reach 100% completeness.

TABLE 2.5. Percentages attributed to regions of the body based on the Character Completeness method for the four sauropodomorph phylogenies used in this study. Average values are shown in Table 2.4 (CCM). See text for details.

Skeletal region	Wilson 2002	Upchurch et al. 2004a	Upchurch et al. 2007a	Yates 2007
Skull	32.47	30.75	33.57	33.71
Cervical vertebrae and ribs	5.98	7.77	5.14	7.37
Dorsal vertebrae and ribs	8.12	13.27	6.85	8.22
Sacral vertebrae and ribs	2.14	2.91	2.05	1.98
Caudal vertebrae and ribs	13.67	9.71	3.42	4.25
Pectoral girdle	3.85	4.53	2.40	1.98

Forelimbs	10.26	8.09	12.67	11.05
Pelvic girdle	5.13	6.15	10.96	9.63
Hindlimbs	16.24	15.53	19.86	20.96
Miscellaneous	2.14	1.29	3.08	0.85

Averages versus ratios

In order to evaluate how the completeness of sauropodomorph specimens has fluctuated through geological or historical time, some form of overall score is required for each time bin that summarises the completeness scores gathered from individual taxa. One approach is to calculate the ratio of 'good' to 'poor' specimens per time bin (e.g. Benton 2008b). However, even if the criteria for assigning specimens to good and poor categories are clearly defined (e.g. a good specimen is one where the skull or skeleton is at least 50% complete [Benton 2008b]), the boundary between these two categories is still based on an arbitrary decision. The danger with ratios is that a decision to draw the boundary between 'good' and 'poor' in a different place (e.g. 'good' equals at least 60% complete) may result in different conclusions. An alternative, non-arbitrary, approach is to calculate the average completeness score for each time bin, as in the following example for the Rhaetian stage. Five sauropodomorph genera are known from the Rhaetian (*Asylosaurus*, *Camelotia*, *Isanosaurus*, *Pantydraco* and *Thecodontosaurus*; note that the same taxa are present in the early and late Rhaetian). Using SCM1, the completeness of the most complete specimen is known for the first four of these taxa. By summing the completeness of these specimens (20%, 9%, 7% and 45% respectively; note the exclusion of *Thecodontosaurus*) and then dividing this value by the number of taxa (i.e. four) an average SCM1 score of 20.25% is calculated for the Rhaetian. By following the same procedure, but using SCM2 instead (which allows the inclusion of Thecodontosaurus), the average SCM2 score for the Rhaetian is 28.8% (20% + 9% + 7% + 46% + 62%; divided by five).

Both average and ratio completeness scores can create apparently anomalous results and it is important to consider which aspects of fossil record quality these summary scores do and do not capture. It should be appreciated that two time bins could have the same average or ratio score, and yet the total number of specimens and taxa found within each could be radically different. In the case of average completeness scores, however, this problem can be addressed by providing information on the variation about the mean value. Therefore, the standard error of the estimate of the mean is determined for each averaged completeness score.

Average and ratio completeness scores do not capture information on the absolute numbers of taxa or specimens known from each time bin: rather, they provide a proxy estimation of the probable level of completeness of a given specimen derived from that time bin. Thus, caution is required when interpreting the meaning of fluctuations in completeness scores through time. This issue is considered further in the Discussion (Chapter 5).

Statistical tests

Three different statistical tests have been utilised to assess the degree of correlation between each completeness curve for the various metrics (Hammer and Harper 2006). Spearman's rank correlation coefficient and Kendall's tau rank correlation have both been used (see above). The third test, Pearson's product-moment correlation coefficient, is a parametric measure for quantifying the amount of linear correlation between two variables (Hammer and Harper 2006). The latter test requires that the data be log-transformed prior to calculation. An additional test (the runs test) has been used to investigate the null hypothesis of total randomness and independence between data points for a time series (Davis 1986; Hammer and Harper 2006). Runs tests require a minimum of ten data points for implementation in PAST, which was used to calculate all statistics (Hammer *et al*. 2001). Lastly, to compensate for the issue of multiple tests,

the Bonferroni correction was applied to pairwise comparisons, which lowers the significance value (see above). This divides the usual *p*-value cut-off of 0.05 by the number of tests implemented. This correction was applied separately to the geological and historical tests because they represent independent data sets.

Palaeolatitudinal patterns

In order to investigate the palaeolatitudinal patterns of a group of organisms, information is required on both their spatial and temporal distribution. The global database has been filtered to include all known sauropod occurrences, including both tracksites and body fossils. Data on ornithischian occurrences have also been included (see above), as well as taxic diversity estimates for each clade and the numbers of dinosaur-bearing collections (DBCs). All co-ordinate data have been converted into palaeolatitudes using the PointTracker software of Scotese (2004). However, the Early and Middle Jurassic has been considered as one time bin as a consequence of the PointTracker software only providing palaeolatitudinal conversions for one time interval (180 Ma) during these two epochs. Mean average palaeolatitudes have been calculated separately for the Northern and Southern Hemispheres.

Palaeolatitudinal sampling biases

It is possible that any palaeolatitudinal patterns that are recovered may merely reflect the influence of some type of sampling bias in the fossil record, perhaps due to workers targeting certain regions more than others (e.g. for ease of accessibility or because this region has produced abundant material before). As such, some attempt must be made to try and correct for any potential palaeolatitudinal sampling biases. To this end, DBCs have been utilised, with these data split into palaeolatitudinal bins (at both 5° and 10° intervals) for each of the epoch level time bins outlined above (i.e. the Early-Middle Jurassic, Late Jurassic, Early Cretaceous and Late Cretaceous). The abundance and diversity data have also been split into these palaeolatitudinal bins, with statistical tests implemented to look for correlations with DBCs. Residuals have been implemented (see above) in an attempt to 'remove' the effects of the rock record, leaving a residual 'unexplained palaeolatitudinal pattern' that cannot be explained in terms of sampling bias. This residuals method has been applied to the tracksite abundance and diversity

data only, as these are the only two datasets with full temporal coverage for both clades.

Statistical tests

The Shapiro-Wilk test has been utilised to investigate whether a sample has been taken from a population with normal distribution (Hammer and Harper 2006). The null hypothesis of normality can be rejected if *p*-values are below the significance level ($p < 0.05$). Details of its calculation are given in Royston (1995). Spearman's rank and Kendall's tau have been used to compare palaeolatitudinal curves and DBCs (see above).

Tracksite abundance

Data on sauropod tracksites have been extracted from the database. Of the 190 tracksites analysed by Lockley *et al*. (1994), just 13 (6.8%) were found in Early-Middle Jurassic or Late Cretaceous deposits. The updated dataset contains 283 sauropod tracksites, with 50 (17.7%) occurring in these previously under-represented epochs. Several countries have had sauropod tracksites discovered in them for the first time only since the Lockley *et al*. (1994) study, with Canada, France, Mexico, Pakistan, Poland, Yemen and Zimbabwe all adding to our knowledge of sauropod distribution. Furthermore, many new sites have added greatly to our understanding of sauropod ecology, biomechanics and evolution, such as the Ardley site in Oxfordshire, UK (Day *et al.* 2002, 2004). Only Jurassic and Cretaceous tracksites have been included in this study; this is because very few Late Triassic tracksites have been conclusively demonstrated to have been produced by sauropods (Wilson 2005b). Whereas the analyses of environmental associations were restricted to incorporating only trackway data that could be assigned to either “narrow-gauge” or “wide-gauge”, these analyses of tracksite abundance use all tracks that can be assigned to Sauropoda. These additional, “indeterminate”, tracksites account for one third of the total tracksite dataset.

Statistical tests

As with previous analyses (see above), Spearman’s rank and Kendall’s tau have been used to compare abundance curves with sampling proxies, etc.

Taphonomy

Only sauropodomorph individuals with information on which elements are preserved have been incorporated into these analyses. These data have been extracted from the sauropodomorph database: the resultant dataset consists of 1203 individuals. Following a slightly modified version of the 'Skeletal Completeness Metric' (SCM: see above), the body has been divided up as follows: skull, teeth (without other cranial elements preserved), cervical, dorsal, sacral and caudal vertebrae, pectoral and pelvic girdle, forelimbs, hindlimbs and osteoderms. For each individual, a simple presence or absence criterion has been used for each region of the body, with these values then summed to determine the total number of individuals preserving each region. Individuals have been considered articulated (see Chapter 8) if at least two elements of the skeleton were in articulation at the time of its discovery. However, it should be noted that there may be problems with using this completeness metric for taphonomic studies, because the completeness of a specimen in a collection is influenced by more than just taphonomy. Erosion and weathering will often remove and destroy elements before a specimen can be discovered and collected. Additionally, parts of skeletons may be left behind in the field because of transportation difficulties or through interest in only collecting skulls. Thus, there are limitations to this type of analysis, although similar problems pervade other attempts to investigate the effects of taphonomic processes on organisms (e.g. taphonomic categories such as those used by Dodson [1971] and Sander [1992]).

Statistical tests

Chi-square tests (see above) have been implemented to investigate the statistical significance of any recovered differences between sauropodomorph groupings, with the cut-off for statistical significance set at 0.05. Only those results that pass this test are reported in the text, except where otherwise stated.

CHAPTER THREE

ENVIRONMENTAL ASSOCIATIONS

Parts of this chapter form the basis for the following paper:

Mannion, P. D. and Upchurch, P. 2010. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36, 253-282.

Analyses and Results

Introduction

The 148 environmental analyses outlined below have been divided into four groups. The whole Mesozoic dataset is used in the first set of analyses (nos. 1-14, Table 3.1) in an attempt to determine whether wide-gauge trackways and titanosaurs (or one of the slightly more inclusive groups) occur more often than expected in either inland or coastal environments. Because these analyses are based on the largest quantity of data available, they are given the greatest weight in the Discussion. The second (nos. 15-115, Tables 3.2-3.8) and third sets of analyses (nos. 116-134, Table 3.9) examine the effects of time-slicing and jack-knifing (through removal of tracks from Korea and the USA) the dataset, respectively. The fourth set of analyses (nos. 135-148, Table 3.10) re-investigates Analyses 1-14, but splits these up to test the null hypothesis of even distribution across environments for each group separately.

Many of the time-sliced analyses are independent of one other: for example, the Bathonian and Callovian stage datasets (e.g. Analyses 45 and 46) share no data points. Similarly, analyses based on trackway data (e.g. Analyses 2 and 5) are independent of those based solely on body fossil data (e.g. Analyses 1 and 4). However, many analyses are wholly or partly non-independent: for example, the analysis of all body fossil localities (no. 4, Table 3.1) shares a substantial amount of data with the analysis of Cretaceous body fossil localities (e.g. no. 18, Table 3.2). The amount of data supporting each statistically significant result, and the independence of separate analyses, will be considered when evaluating the implications of these results in the Discussion.

Analyses 1-14 – Mesozoic datasets

Titanosaurs versus non-titanosaurs

Analyses 1-6 (Table 3.1) compare the distributions of titanosaur and non-titanosaur body fossils, narrow-gauge and wide-gauge trackways, and body fossils plus trackways, based on estimated numbers of individuals (Analyses 1-3) and localities (Analyses 4-6). Analyses 1, 2, 4 and 5 produce very low *p*-values ($p = 1x10^{-5}$ to $8x10^{-5}$), whereas Analyses 3 ($p = 7x10^{-4}$) and 6 ($p < 0.0677$) are non-significant. The significant results suggest that titanosaurs and wide-gauge tracks occur more often than expected in inland environments, whereas non-titanosaurs and narrow-gauge trackways occur more often than expected in coastal environments. Analysis 3, although non-significant, indicates the reverse association.

Titanosauriforms versus non-titanosauriforms

Analyses 7-10 (Table 3.1) examine environmental associations among titanosauriform and non-titanosauriform body fossil data by themselves and with the trackway data added, based on estimates of both numbers of individuals and localities.

TABLE 3.1. Summary of analyses (1-14) of potential environmental associations among sauropods, based on the complete Mesozoic datasets. Abbreviations: E=expected number; O=observed number; T=total number. The following symbols next to an analysis number denote: (1) an asterisk (*) denotes a significant result which supports titanosaurs preferring inland environments; (2) two asterisks (**) denote a significant result which supports titanosaurs preferring coastal environments; (3) a hash sign (#) denotes a significant result which supports titanosauriforms preferring inland environments; (4) two hash signs (##) denote a significant result which supports

titanosauriforms preferring coastal environments. Significant results are those with *p*-levels that are less than 3.78 x10^{-4}.

Analysis No.	**Comparison**	**Inland**	**Coastal**	***p*-value**
1*	Body fossil individuals: T = 1360	T = 1226	T = 134	< 1x10^{-5}
	Non-titanosaurs: T = 987	O = 864 E = 889.75	O = 123 E = 97.25	
	Titanosaurs: T = 373	O = 362 E = 336.25	O = 11 E = 36.75	
2*	Trackway individuals: T = 633	T = 236	T = 397	< 1x10^{-5}
	Narrow-gauge: T = 187	O = 30 E = 69.72	O = 157 E = 117.28	
	Wide-gauge: T = 446	O = 206 E = 166.28	O = 240 E = 279.72	
3	Body fossil and trackway individuals: T = 1993	T = 1462	T = 531	7x10^{-4}
	Non-titanosaurs and narrow-gauge: T = 1174	O = 894 E = 861.21	O = 280 E = 312.79	
	Titanosaurs and wide-gauge: T = 819	O = 568 E = 600.79	O = 251 E = 218.21	
4*	Body fossil localities: T = 706	T = 624	T = 82	< 1x10^{-5}
	Non-titanosaurs: T = 479	O = 404 E = 423.37	O = 75 E = 55.63	
	Titanosaurs: T = 237	O = 227 E = 209.47	O = 10 E = 27.53	
5*	Trackway localities: T = 190	T = 116	T = 74	8x10^{-5}
	Narrow-gauge: T = 41	O = 14 E = 25.03	O = 27 E = 15.97	
	Wide-gauge: T = 150	O = 102 E = 91.58	O = 48 E = 58.42	
6	Body fossil and trackway localities: T = 896	T = 740	T = 156	0.0677
	Non-titanosaurs and narrow-gauge: T = 520	O = 418 E = 429.46	O = 102 E = 90.54	
	Titanosaurs and wide-gauge: T = 387	O = 329 E = 319.62	O = 58 E = 67.38	
7	Body fossil individuals: T = 1360	T = 1226	T = 134	0.2145
	Non-titanosauriforms: T = 819	O = 745 E = 738.30	O = 74 E = 80.70	
	Titanosauriforms: T = 541	O = 481	O = 60	

		E = 487.70	E = 53.30	
8##	Body fossil and trackway individuals: T = 1993	T = 1462	T = 531	$2x10^{-4}$
	Non-titanosauriforms and narrow-gauge: T = 1006	O = 775 E = 737.97	O = 231 E = 268.03	
	Titanosauriforms and wide-gauge: T = 987	O = 687 E = 724.03	O = 300 E = 262.97	
9	Body fossil localities: T = 706	T = 624	T = 82	0.1296
	Non-titanosauriforms: T = 370	O = 323 E = 327.03	O = 47 E = 42.97	
	Titanosauriforms: T = 359	O = 309 E = 317.30	O = 50 E = 41.70	
10	Body fossil and trackway localities: T = 896	T = 740	T = 156	0.2537
	Non-titanosauriforms and narrow-gauge: T = 411	O = 337 E = 339.44	O = 74 E = 71.56	
	Titanosauriforms and wide-gauge: T = 509	O = 411 E = 420.38	O = 98 E = 88.62	
11*	Body fossil individuals: T = 541	T = 481	T = 60	$< 1x10^{-5}$
	Non-titanosaurian titanosauriforms: T = 168	O = 119 E = 149.37	O = 49 E= 18.63	
	Titanosaurs: T = 373	O = 362 E = 331.63	O = 11 E = 41.37	
12*	Body fossil localities: T = 362	T = 310	T = 52	$< 1x10^{-5}$
	Non-titanosaurian titanosauriforms: T = 122	O = 82 E = 104.48	O = 40 E = 17.52	
	Titanosaurs: T = 237	O = 227 E = 202.96	O = 10 E = 34.04	
13	Body fossil individuals: T = 1360	T = 1225	T = 135	0.9383
	Non-macronarians: T = 565	O = 509 E = 508.92	O = 56 E = 56.08	
	Macronarians: T = 795	O = 716 E = 716.08	O = 79 E = 78.92	
14	Body fossil localities: T = 706	T = 624	T = 82	0.5435
	Non-macronarians: T = 307	O = 268 E = 271.34	O = 39 E = 35.66	
	Macronarians: T = 467	O = 412 E = 412.76	O = 55 E = 54.24	

Three of these analyses (7, 9 and 10) fail to produce statistically significant results (p = 0.1296 to 0.2537). However, Analysis 8, which combines body fossil and trackway data

for individuals, produces a significantly low *p*-value ($p = 2x10^{-4}$). The latter result suggests that titanosauriforms occur more often than expected in coastal environments, whereas non-titanosauriforms occur more often than expected in inland environments (the reverse of the environmental association found among titanosaurs and non-titanosaurs). It is possible that this reversal occurs because the data from non-titanosaurian titanosauriforms are somehow 'swamping' the inland signal recovered in Analyses 1-5 (see below).

Titanosaurs versus non-titanosaurian ('basal') titanosauriforms

To test for this 'swamping' of the titanosaur signal by non-titanosaurian titanosauriforms, Analyses 11 and 12 (Table 3.1) have been implemented. These restrict the body fossil dataset to Titanosauriformes, partitioning the data into titanosaurs and non-titanosaurs. Both analyses display strong support ($p < 1x10^{-5}$) for titanosaurs and basal titanosauriforms occurring more often than expected in inland and coastal environments, respectively.

Macronarians versus non-macronarians

Analyses 13 and 14 (Table 3.1) compare the distributions of macronarians and non-macronarians. Both analyses fail the chi-square test (Table 3.1), indicating that there is no significant support for environmental associations when sauropods are partitioned into Macronaria versus non-Macronaria (contra Butler and Barrett 2008: see below).

Analyses 15-115 - time-slicing the data

Cretaceous time-slices

Analyses 15-17 (Table 3.2) repeat Analyses 1, 5 and 7 respectively, but are restricted to Cretaceous sauropods. Analyses 15 and 17 pass the chi-square tests ($p < 1x10^{-5}$), whereas Analysis 16 fails. These results mean that the restriction of the dataset to Cretaceous sauropods does not affect conclusions based on Analysis 1. Analysis 5 supported a positive association between wide-gauge trackways and inland environments and narrow-gauge trackways and coastal environments, but this result disappears when only Cretaceous data are examined (Analysis 16), probably as a result of the paucity of narrow-gauge trackways known from the Cretaceous (six in the dataset). Analysis 7 failed the chi-square test, but when only Cretaceous forms are examined in Analysis 17, support for a positive association between titanosauriforms and inland environments and non-titanosauriforms and coastal environments is obtained. This result probably occurs because the restriction of 'Titanosauriformes' to Cretaceous taxa alone means that this category comprises a higher proportion of titanosaurs.

TABLE 3.2. Summary of analyses (15-29) of potential environmental associations among sauropods, based on larger time-slices such as 'Cretaceous', 'Early Cretaceous', etc. (see 'Analyses and Results' for details). For abbreviations and symbols, see legend to Table 3.1.

Analysis No.	**Comparison**	**Inland**	**Coastal**	***p*-value**
15*	Body fossil individuals (Cretaceous only): T = 526	T = 499	T = 27	$< 1x10^{-5}$
	Non-titanosaurs: T = 152	O = 131 E = 144.20	O = 21 E = 7.80	
	Titanosaurs: T = 374	O = 368 E = 354.80	O = 6 E = 19.20	
16	Trackway localities (Cretaceous only): T = 131	T = 97	T = 34	0.6748
	Narrow-gauge: T = 6	O = 4 E = 4.44	O = 2 E = 1.56	
	Wide-gauge: T = 125	O = 93	O = 32	

		E = 92.56	E = 32.44	
17#	Body fossil individuals (Cretaceous only): T = 526	T = 499	T = 27	$< 1x10^{-5}$
	Non-titanosauriforms: T = 65	O = 54 E = 61.66	O = 11 E = 3.34	
	Titanosauriforms: T = 461	O = 445 E = 437.34	O = 16 E = 23.66	
18	Body fossil localities (Cretaceous only): T = 525	T = 496	T = 29	0.0574
	Non-macronarians: T = 54	O = 48 E = 51.02	O = 6 E = 2.98	
	Macronarians: T = 471	O = 448 E = 444.98	O = 23 E = 26.02	
19	Body fossil localities (Cretaceous only): T = 334	T = 312	T = 22	0.1351
	Non-macronarians: T = 41	O = 36 E = 38.30	O = 5 E = 2.70	
	Macronarians: T = 297	O = 279 E = 277.44	O = 18 E = 19.56	
20	Body fossil localities (Butler and Barrett Cretaceous data): T = 175	T = 166	T = 9	0.0019
	Non-titanosaurs: T = 78	O = 69 E = 73.99	O = 9 E = 4.01	
	Titanosaurs: T = 123	O = 121 E = 116.67	O = 2 E= 6.33	
21	Body fossil and trackway localities (Butler and Barrett Cretaceous data): T = 177	T = 168	T = 9	0.0017
	Non-titanosaurs and narrow-gauge: T = 78	O = 69 E = 74.03	O = 9 E = 3.97	
	Titanosaurs and wide-gauge: T = 125	O = 123 E = 118.64	O = 2 E = 6.36	
22	Body fossil localities (Butler and Barrett Cretaceous data): T = 175	T = 166	T = 9	0.0178
	Non-titanosauriforms: T = 27	O = 23 E = 25.61	O = 4 E = 1.39	
	Titanosauriforms: T = 174	O = 167 E = 165.05	O = 7 E = 8.95	
23	Body fossil and trackway localities (Butler and Barrett Cretaceous data): T = 177	T = 168	T = 9	0.0163
	Non-titanosauriforms and narrow-gauge: T = 27	O = 23 E = 25.63	O = 4 E = 1.37	

	Titanosauriforms and wide-gauge: T = 176	O = 169 E = 167.05	O = 7 E = 8.95	
24*	Body fossil individuals (Early-mid Cretaceous only): T = 259	T = 237	T = 22	$1x10^{-4}$
	Non-titanosaurs: T = 135	O = 115 E = 123.53	O = 20 E = 11.47	
	Titanosaurs: T = 124	O = 122 E = 113.47	O = 2 E = 10.53	
25	Trackway individuals (Early-mid-Cretaceous): T = 284	T = 180	T = 104	0.2769
	Narrow-gauge: T = 3	O = 1 E = 1.9	O = 2 E = 1.1	
	Wide-gauge: T = 281	O = 179 E = 178.1	O = 102 E = 102.9	
26	Body fossil and trackway individuals (Early-mid- Cretaceous): T = 543	T = 417	T = 126	0.0193
	Non-titanosaurs and narrow-gauge: T = 138	O = 116 E = 105.98	O = 22 E = 32.02	
	Titanosaurs and wide-gauge: T = 405	O = 301 E = 311.02	O = 104 E = 93.98	
27	Body fossil localities (Early-mid Cretaceous): T = 162	T = 144	T = 18	0.0039
	Non-titanosaurs: T = 95	O = 79 E = 84.44	O = 16 E = 10.56	
	Titanosaurs: T = 73	O = 71 E = 64.89	O = 2 E = 8.11	
28	Trackway localities (Early-mid Cretaceous): T = 120	T = 88	T = 32	0.1126
	Narrow-gauge: T = 3	O = 1 E = 2.20	O = 2 E = 0.80	
	Wide-gauge: T = 117	O = 87 E = 85.80	O = 30 E = 31.20	
29	Body fossil and trackway localities (Early-mid- Cretaceous): T = 282	T = 232	T = 50	0.7195
	Non-titanosaurs and narrow-gauge: T = 98	O = 80 E = 80.62	O = 18 E = 17.38	
	Titanosaurs and wide-gauge: T = 190	O = 158 E = 156.31	O = 32 E = 33.69	

Analyses 18 and 19 examine the distributions of macronarians and non-macronarians based on just the Cretaceous part of the dataset. Both analyses fail the chi-square test

(Table 3.2), indicating that there is no support for environmental associations when sauropods are partitioned into these taxonomic divisions. It should be noted, however, that the *p*-values for the 'Cretaceous only' analyses ($p < 0.14$) are substantially lower than those obtained when all sauropods are considered in Analyses 13 and 14 ($p > 0.5$). This phenomenon is likely to occur because the taxonomic content of 'Cretaceous Macronaria' is very similar to that of Titanosauriformes and Titanosauria.

Butler and Barrett's (2008) dataset contains information solely on Cretaceous sauropods and therefore represents a time-slice of the total available data. Analyses 20-23 examine environmental associations between titanosaurs and non-titanosaurs, and between titanosauriforms and non-titanosauriforms, using this dataset. Although all of these analyses are consistent with positive associations between titanosaurs/titanosauriforms and inland environments, none passes the chi-square test ($p > 0.0017$: Table 3.2).

Within Cretaceous time-slices

Analyses 24-29 (Table 3.2) repeat Analyses 1-6, but with the data restricted to the Early and early Late Cretaceous (Berriasian-Coniacian). Analyses 25-29 produce non-significant *p*-values. However, the remaining analysis (24: body-fossil individuals) still supports the positive association between titanosaurs and inland environments ($p = 1 \times 10^{-4}$).

Stage level time-slicing

Analyses 30-115 (Tables 3.3-3.8) replicate Analyses 1-6, but in each case the data are restricted to just one of the Jurassic or Cretaceous geological stages. Of these 86 analyses, 64 failed to produce statistically significant results; 13 produced a significant result in favour of a negative association between titanosaurs and/or wide gauge

trackways and inland environments; and nine produced significant results in favour of a positive association between titanosaurs and/or wide gauge trackways and inland environments. Although these results may appear collectively equivocal, it should be noted that 12 of the 13 results favouring a negative association between titanosaurs and/or wide-gauge trackways and inland environments are obtained from analyses of Middle and Late Jurassic stages (the exception is Analysis 66 – Albian body fossil and trackway individuals), whereas all nine analyses supporting the positive association with inland environments are obtained for Cretaceous stages. These results reflect the fact that the earliest wide-gauge trackways (e.g. the Middle Jurassic Ardley site) and the earliest titanosaurian body fossils (*Janenschia*, from the Late Jurassic of Tendaguru, Tanzania) are preserved in coastal environments (Aberhan *et al*. 2002; Day *et al*. 2002, 2004) (see Discussion). Many statistically significant environmental associations occur even when the dataset is time-sliced to stage level, suggesting that the results cannot be explained merely as an artefact created by uneven sampling of the two environment types from deposits of Jurassic and Cretaceous age (see 'Materials and Methods').

TABLE 3.3. Results of Analyses 30-43 (sauropod body fossil individuals) per European stage. Only stages where both titanosaurs and non-titanosaur body fossils are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis no.	**Stage**	**Non-titanosaurs**		**Titanosaurs**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
30**	Kimmeridgian	O = 582 E = 576.42	O = 38 E = 43.58	O = 0 E = 5.58	O = 6 E = 0.42	$< 1x10^{-5}$
31**	Tithonian	O = 489 E = 482.10	O = 70 E = 76.90	O = 0 E = 6.90	O = 8 E = 1.10	$< 1x10^{-5}$
32	Berriasian	O = 20 E = 20.00	O = 0 E = 0	O = 6 E = 6.00	O = 0 E = 0	1
33	Valanginian	O = 13 E = 13.00	O = 0 E = 0	O = 19 E = 19.00	O = 0 E = 0	1
34	Hauterivian	O = 35 E = 36.36	O = 4 E = 2.64	O = 20 E = 18.64	O = 0 E = 1.36	0.1371
35	Barremian	O = 52	O = 13	O = 33	O = 0	0.0058

		E = 56.38	E = 8.62	E = 28.62	E = 4.38	
36	Aptian	O = 50 E = 52.00	O = 6 E = 4.00	O = 28 E = 26.00	O = 0 E = 2.00	0.0723
37	Albian	O = 61 E = 62.23	O = 4 E = 2.77	O = 29 E = 27.77	O = 0 E = 1.23	0.1733
38	Cenomanian	O = 23 E = 23.21	O = 1 E = 0.79	O = 36 E = 35.79	O = 1 E = 1.21	0.7567
39	Turonian	O = 11 E = 11.00	O = 0 E = 0	O = 52 E = 52.00	O = 0 E = 0	1
40	Coniacian	O = 5 E = 5.00	O = 0 E = 0	O = 51 E = 51.00	O = 0 E = 0	1
41	Santonian	O = 3 E = 3.00	O = 0 E = 0	O = 46 E = 46.00	O = 0 E = 0	1
42	Campanian	O = 4 E = 3.94	O = 0 E = 0.06	O = 126 E = 126.06	O = 2 E = 1.94	0.8018
43*	Maastrichtian	O = 5 E = 9.75	O = 5 E = 0.25	O = 189 E = 184.25	O = 0 E = 4.75	$< 1x10^{-5}$

TABLE 3.4. Results of Analyses 44-55 (sauropod tracksite individuals) per European stage. Only stages where both titanosaurs and non-titanosaurs are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis No.	**Stage**	**Narrow-gauge**		**Wide-gauge**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
44**	Bajocian	O = 8 E = 3.56	O = 4 E = 8.44	O = 0 E = 4.44	O = 15 E = 10.56	$2x10^{-4}$
45**	Bathonian	O = 17 E = 9.83	O = 31 E = 38.17	O = 0 E = 7.17	O = 35 E = 27.83	$8x10^{-5}$
46	Callovian	O = 8 E = 8.31	O = 4 E = 3.69	O = 1 E = 0.69	O = 0 E = 0.31	0.4857
47	Kimmeridgian	O = 8 E = 12.36	O = 70 E = 65.64	O = 8 E = 3.64	O = 15 E = 19.36	0.0046
48	Tithonian	O = 3 E = 7.33	O = 91 E = 86.67	O = 8 E = 3.67	O = 39 E = 43.33	0.0039
49	Berriasian	O = 0 E = 0.79	O = 1 E = 0.21	O = 34 E = 33.21	O = 8 E = 8.79	0.0497
50*	Valanginian	O = 0 E = 0.94	O = 1 E = 0.06	O = 32 E = 31.06	O = 1 E = 1.94	$6x10^{-5}$
51*	Hauterivian	O = 0 E = 0.94	O = 1 E = 0.06	O = 32 E = 31.06	O = 1 E = 1.94	$6x10^{-5}$

52*	Barremian	O = 0 E = 0.98	O = 1 E = 0.02	O = 41 E = 40.02	O = 0 E = 0.98	$< 1x10^{-5}$
53*	Aptian	O = 0 E = 0.98	O = 1 E = 0.02	O = 100 E = 99.02	O = 1 E = 0.98	$< 1x10^{-5}$
54	Albian	O = 1 E = 0.62	O = 0 E = 0.38	O = 137 E = 137.38	O = 86 E = 85.62	0.4337
55	Campanian	O = 3 E = 1.83	O = 0 E = 1.17	O = 11 E = 12.17	O = 9 E = 7.83	0.1376

TABLE 3.5. Results of Analyses 56-72 (sauropod body fossil and tracksite individuals) per European stage. Only stages where both titanosaurs and non-titanosaurs are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis no.	**Stage**	**Non-titanosaurs and narrow-gauge**		**Titanosaurs and wide-gauge**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
56**	Bajocian	O = 52 E = 41.01	O = 4 E = 14.99	O = 0 E = 10.99	O = 15 E = 4.01	$< 1x10^{-5}$
57**	Bathonian	O = 90 E = 70.06	O = 33 E = 52.94	O = 0 E = 19.94	O = 35 E = 15.06	$< 1x10^{-5}$
58	Callovian	O = 89 E = 89.04	O = 4 E = 3.96	O = 1 E = 0.96	O = 0 E = 0.04	0.8376
59**	Kimmeridgian	O = 590 E = 574.15	O = 108 E = 123.85	O = 8 E = 23.85	O = 21 E = 5.15	$< 1x10^{-5}$
60**	Tithonian	O = 492 E = 461.16	O = 161 E = 191.84	O = 8 E = 33.84	O = 47 E = 16.16	$< 1x10^{-5}$
61	Berriasian	O = 20 E = 18.26	O = 1 E = 2.74	O = 40 E = 41.74	O = 8 E = 6.26	0.1416
62	Valanginian	O = 13 E = 13.58	O = 1 E = 0.42	O = 51 E = 50.42	O = 1 E = 1.58	0.3078
63	Hauterivian	O = 35 E = 37.42	O = 5 E = 2.58	O = 52 E = 49.58	O = 1 E = 3.42	0.0391
64*	Barremian	O = 52 E = 59.40	O = 14 E = 6.60	O = 74 E = 66.60	O = 0 E = 7.40	$3x10^{-5}$
65*	Aptian	O = 50 E = 54.55	O = 7 E = 2.45	O = 128 E = 123.45	O = 1 E = 5.55	$3x10^{-4}$
66**	Albian	O = 62 E = 47.32	O = 4 E = 18.68	O = 166 E = 180.68	O = 86 E = 71.32	$< 1x10^{-5}$
67	Cenomanian	O = 23 E = 21.82	O = 1 E = 2.18	O = 37 E = 38.18	O = 5 E = 3.82	0.2943

68	Turonian	O = 11 E = 10.72	O = 0 E = 0.28	O = 65 E = 65.28	O = 2 E = 1.72	0.5633
69	Coniacian	O = 5 E = 4.86	O = 0 E = 0.14	O = 64 E = 64.14	O = 2 E = 1.86	0.6938
70	Santonian	O = 3 E = 3.00	O = 0 E = 0	O = 46 E = 46.00	O = 0 E = 0	1
71	Campanian	O = 7 E = 6.50	O = 0 E = 0.50	O = 137 E = 137.50	O = 11 E = 10.50	0.4527
72	Maastrichtian	O = 5 E = 7.93	O = 5 E = 2.07	O = 202 E = 199.07	O = 49 E = 51.93	0.0198

TABLE 3.6. Results of Analyses 73-86 (sauropod body fossil localities) per European stage. Only stages where both titanosaurs and non-titanosaurs are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis No.	**Stage**	**Non-titanosaurs**		**Titanosaurs**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
73**	Kimmeridgian	O = 235 E = 233.10	O = 23 E = 24.90	O = 0 E = 4.52	O = 5 E = 0.48	$< 1x10^{-5}$
74**	Tithonian	O = 225 E = 222.57	O = 50 E = 52.43	O = 0 E = 5.67	O = 7 E = 1.33	$< 1x10^{-5}$
75	Berriasian	O = 17 E = 17.00	O = 0 E = 0	O = 6 E = 6.00	O = 0 E = 0	1
76	Valanginian	O = 10 E = 10.00	O = 0 E = 0	O = 15 E = 15.00	O = 0 E = 0	1
77	Hauterivian	O = 22 E = 24.70	O = 4 E = 1.30	O = 16 E = 15.2	O = 0 E = 0.8	0.0094
78	Barremian	O = 34 E = 36.8	O = 12 E = 9.20	O = 15 E = 12.00	O = 0 E = 3.00	0.0282
79	Aptian	O = 32 E = 34.07	O = 6 E = 3.93	O = 22 E = 19.72	O = 0 E = 2.28	0.0525
80	Albian	O = 42 E = 43.17	O = 4 E = 2.83	O = 23 E = 21.58	O = 0 E = 1.42	0.1552
81	Cenomanian	O = 19 E = 19.05	O = 1 E = 0.95	O = 26 E = 25.71	O = 1 E = 1.29	0.7153
82	Turonian	O = 10 E = 10.00	O = 0 E = 0	O = 41 E = 41.00	O = 0 E = 0	1
83	Coniacian	O = 4 E = 4.00	O = 0 E = 0	O = 40 E = 40.00	O = 0 E = 0	1
84	Santonian	O = 2	O = 0	O = 40	O = 0	1

		E = 2.00	E = 0	E = 40.00	E = 0	
85	Campanian	O = 3 E = 2.93	O = 0 E = 0.07	O = 81 E = 80.98	O = 2 E = 2.02	0.7592
86*	Maastrichtian	O = 4 E = 5.90	O = 2 E = 0.10	O = 113 E = 111.08	O = 0 E = 1.92	$< 1x10^{-5}$

TABLE 3.7. Results of Analyses 87-98 (sauropod tracksite localities) per European stage. Only stages where both titanosaurs and non-titanosaurs are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis no.	**Stage**	**Narrow-gauge**		**Wide-gauge**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
87	Bajocian	O = 1 E = 0.67	O = 1 E = 1.33	O = 0 E = 0.33	O = 1 E = 0.67	0.3913
88	Bathonian	O = 6 E = 5.57	O = 7 E = 7.43	O = 0 E = 0.86	O = 2 E = 1.14	0.2106
89	Callovian	O = 1 E = 1.33	O = 1 E = 0.67	O = 1 E = 0.67	O = 0 E = 0.33	0.3871
90	Kimmeridgian	O = 4 E = 4.20	O = 8 E = 7.80	O = 3 E = 2.80	O = 5 E = 5.20	0.8495
91	Tithonian	O = 3 E = 4.00	O = 9 E = 8.00	O = 6 E = 5.00	O = 9 E = 10.00	0.4113
92	Berriasian	O = 0 E = 0.70	O = 1 E = 0.30	O = 7 E = 6.30	O = 2 E = 2.70	0.1073
93	Valanginian	O = 0 E = 0.75	O = 1 E = 0.25	O = 6 E = 5.25	O = 1 E = 1.75	0.0641
94	Hauterivian	O = 0 E = 0.75	O = 1 E = 0.25	O = 6 E = 5.25	O = 1 E = 1.75	0.0641
95*	Barremian	O = 0 E = 0.92	O = 1 E = 0.08	O = 11 E = 10.08	O = 0 E = 0.92	$3x10^{-4}$
96*	Aptian	O = 0 E = 0.96	O = 1 E = 0.04	O = 49 E = 48.04	O = 1 E = 1.96	$<1x10^{-5}$
97	Albian	O = 1 E = 0.77	O = 0 E = 0.23	O = 78 E = 78.23	O = 24 E = 23.77	0.5826
98	Campanian	O = 3 E = 2.14	O = 0 E = 0.86	O = 2 E = 2.86	O = 2 E = 1.14	0.1455

TABLE 3.8. Results of Analyses 99-115 (sauropod tracksite and body fossil localities) per European stage. Only stages where both titanosaurs and non-titanosaurs are known are shown. See Table 3.1 for explanation of abbreviations and symbols.

Analysis No.	**Stage**	**Non-titanosaurs and narrow-gauge**		**Titanosaurs and wide-gauge**		***p*-value**
		Inland	**Coastal**	**Inland**	**Coastal**	
99	Bajocian	O = 16 E = 15.00	O = 1 E = 2.00	O = 0 E = 0.88	O = 1 E = 0.12	0.0049
100	Bathonian	O = 22 E = 21.00	O = 9 E = 10.00	O = 0 E = 1.35	O = 2 E = 0.65	0.0381
101	Callovian	O = 21 E = 20.95	O = 1 E = 1.05	O = 1 E = 0.95	O = 0 E = 0.05	0.8144
102**	Kimmeridgian	O = 239 E = 241.86	O = 31 E = 38.14	O = 3 E = 11.23	O = 10 E = 1.77	$<1x10^{-5}$
103**	Tithonian	O = 228 E = 220.19	O = 59 E = 66.81	O = 6 E = 16.88	O = 16 E = 5.12	$<1x10^{-5}$
104	Berriasian	O = 17 E = 16.36	O = 1 E = 1.64	O = 13 E = 13.64	O = 2 E = 1.36	0.3893
105	Valanginian	O = 10 E = 10.33	O = 1 E = 0.67	O = 21 E = 20.67	O = 1 E = 1.33	0.6122
106	Hauterivian	O = 22 E = 24.75	O = 5 E = 2.25	0 = 22 E = 21.08	O = 1 E = 1.92	0.0416
107	Barremian	O = 34 E = 38.51	O = 13 E = 8.49	O = 26 E = 21.31	O = 0 E = 4.69	0.0033
108	Aptian	O = 32 E = 36.14	O = 7 E = 2.86	O = 71 E = 66.72	O = 1 E = 5.28	0.0014
109	Albian	O = 43 E = 39.17	O = 4 E = 7.83	O = 101 E = 104.17	O = 24 E = 20.83	0.0932
110	Cenomanian	O = 19 E = 18.64	O = 1 E = 1.36	O = 27 E = 27.02	O = 2 E = 1.98	0.7494
111	Turonian	O = 10 E = 9.81	O = 0 E = 0.19	O = 45 E = 45.15	O = 1 E = 0.85	0.6383
112	Coniacian	O = 4 E = 3.91	O = 0 E = 0.09	O = 44 E = 44.04	O = 1 E = 0.96	0.7655
113	Santonian	O = 2 E = 2.00	O = 0 E = 0	O = 40 E = 40.00	O = 0 E = 0	1
114	Campanian	O = 6 E = 5.73	O = 0 E = 0.27	O = 83 E = 83.05	O = 4 E = 3.95	0.5941
115*	Maastrichtian	O = 4 E = 5.76	O = 2 E = 0.24	O = 115 E = 114.16	O = 4 E = 4.84	$2x10^{-4}$

Analyses 116-134 - 'Jack-knifing' the data

Following exclusion of the Korean tracksites, environmental associations are not supported by analyses 119-121 (Table 3.9, $p > 0.2432$) based on the number of localities. Analyses 116-118, based on number of individuals, pass the chi-square test ($p < 1x10^{-5}$). Analysis 116 (based on trackway data alone) continues to support the positive associations between wide-gauge trackways and inland environments and narrow-gauge trackways and coastal environments. However, the addition of the body fossil data in Analyses 117 and 118 reverses the polarity of these associations. Analysis 122 explores what happens when the 73 Korean tracksites are treated as six separate localities, but this version of the dataset still fails the chi-square test ($p = 0.23$: Table 3.9).

TABLE 3.9. Results of Analyses 116-134 ('Sensitivity analyses). See Table 3.1 for explanation of abbreviations and symbols.

Analysis No.	**Comparison**	**Inland**	**Coastal**	***p*-value**
116*	Trackway individuals minus Korean data: T = 519	T = 122	T = 397	$< 1x10^{-5}$
	Narrow-gauge: T = 183	O = 26 E = 43.02	O =157 E = 139.98	
	Wide-gauge T = 336	O= 96 E = 78.98	O = 240 E = 257.02	
117**	Body fossil and trackway individuals minus Korean data: T = 1879	T = 1348	T = 531	$< 1x10^{-5}$
	Non-titanosaurs and narrow-gauge: T = 1170	O = 890 E = 839.36	O = 280 E = 330.64	
	Titanosaurs and wide-gauge: T = 709	O = 458 E = 508.64	O = 251 E = 200.36	
118##	Body fossil and trackway individuals minus Korean data: T = 1879	T = 1348	T = 531	$< 1x10^{-5}$
	Non-titanosauriforms and narrow-	O = 771	O = 231	

	gauge: T = 1002	E = 718.84	E = 283.16	
	Titanosauriforms and wide-gauge: T = 877	O = 577 E = 629.16	O = 300 E = 247.84	
119	Trackway localities minus Korean data: T = 117	T = 43	T = 74	0.2432
	Narrow-gauge: T = 38	O = 11 E = 13.97	O = 27 E = 24.03	
	Wide-gauge: T = 80	O = 32 E = 29.40	O = 48 E = 50.60	
120	Body fossil and trackway localities minus Korean data: T = 823	T = 667	T = 156	0.5896
	Non-titanosaurs and narrow-gauge: T = 517	O = 415 E = 419.00	O = 102 E = 98.00	
	Titanosaurs and wide-gauge: T = 317	O = 259 E = 256.91	O = 58 E = 60.09	
121	Body fossil and trackway localities minus Korean data: T = 823	T = 667	T = 156	0.0513
	Non-titanosauriforms and narrow-gauge: T = 396	O = 334 E = 320.94	O = 74 E = 75.06	
	Titanosauriforms and wide-gauge: T = 438	O = 341 E = 354.98	O = 98 E = 83.02	
122	Trackway localities with Korea reduced to the 6 main localities: T = 123	T = 49	T = 74	0.23
	Narrow-gauge: T = 39	O = 12 E = 15.54	O = 27 E = 23.46	
	Wide-gauge: T = 85	O = 37 E = 33.86	O = 48 E = 51.14	
123*	Trackway individuals minus USA data: T = 502	T = 222	T = 280	$< 1x10^{-5}$
	Narrow-gauge: T = 141	O = 27 E = 62.35	O = 114 E = 78.65	
	Wide-gauge: T = 361	O = 195 E = 159.65	O = 166 E = 201.35	
124	Body fossil and trackway individuals minus USA data: T = 1862	T = 1448	T = 414	0.1143
	Non-titanosaurs and narrow-gauge: T = 1128	O = 891 E = 877.20	O = 237 E = 250.80	
	Titanosaurs and wide-gauge: T = 734	O = 557 E = 570.80	O = 177 E = 163.20	
125	Body fossil and trackway individuals minus USA data: T =	T = 1448	T = 414	0.0044

	1862			
	Non-titanosauriforms and narrow-gauge: T = 960	O = 772 E = 746.55	O = 188 E = 213.45	
	Titanosauriforms and wide-gauge: T = 902	O = 676 E = 701.45	O = 226 E = 200.55	
126*	Trackway localities minus USA data: T = 157	T = 107	T = 50	$< 1x10^{-5}$
	Narrow-gauge: T = 34	O = 11 E = 23.17	O = 23 E = 10.83	
	Wide-gauge: T = 124	O = 96 E = 84.51	O = 28 E = 39.49	
127	Body fossil and trackway localities minus USA data: T = 863	T = 731	T = 132	$5x10^{-4}$
	Non-titanosaurs and narrow-gauge: T = 513	O = 415 E = 434.53	O = 98 E = 78.47	
	Titanosaurs and wide-gauge: T = 361	O = 323 E = 305.78	O = 38 E = 55.22	
128	Body fossil and trackway localities minus USA data: T = 863	T = 731	T = 132	0.2121
	Non-titanosauriforms and narrow-gauge: T = 404	334 (342.21)	70 (61.79)	
	Titanosauriforms and wide-gauge: T = 483	O = 405 E = 409.12	O = 78 E = 73.88	
129*	Trackway individuals minus Korean and USA data: T = 388	T = 108	T = 280	$3x10^{-4}$
	Narrow-gauge: T = 137	O = 23 E = 38.13	O = 114 E = 98.87	
	Wide-gauge: T = 251	O = 85 E = 69.87	O = 166 E = 181.13	
130	Body fossil and trackway individuals minus Korean and USA data: T = 1748	T = 1334	T = 414	$6x10^{-4}$
	Non-titanosaurs and narrow-gauge: T = 1124	O = 887 E = 857.79	O = 237 E = 266.21	
	Titanosaurs and wide-gauge: T = 624	O = 447 E = 476.21	O = 177 E = 147.79	
131##	Body fossil and trackway individuals minus Korean and USA data: T = 1748	T = 1334	T = 414	$1x10^{-5}$
	Non-titanosauriforms and narrow-gauge: T = 956	O = 768 E = 729.58	O = 188 E = 226.42	
	Titanosauriforms and wide-gauge: T = 792	O = 566 E = 604.42	O = 226 E = 187.58	

132	Trackway localities minus USA and Korean data: T = 84	T = 34	T = 50	0.0788
	Narrow-gauge: T = 31	O = 8 E = 12.55	O = 23 E = 18.45	
	Wide-gauge: T = 54	O = 26 E = 21.86	O = 28 E = 32.14	
133	Body fossil and trackway localities minus Korean and USA data: T = 790	T = 658	T = 132	0.0241
	Non-titanosaurs and narrow-gauge: T = 510	O = 412 E = 424.78	O = 98 E = 85.22	
	Titanosaurs and wide-gauge: T = 291	O = 253 E = 242.38	O = 38 E = 48.62	
134	Body fossil and trackway localities minus Korean and USA data: T = 790	T = 658	T = 132	0.2102
	Non-titanosauriforms and narrow-gauge: T = 401	O = 331 E = 334.00	O = 70 E = 67.00	
	Titanosauriforms and wide-gauge: T = 413	O = 335 E = 344.00	O = 78 E = 69.00	

Analyses 123-128 (Table 3.9) exclude the USA trackway data. Four of these analyses (124, 125, 127 and 128) fail the chi-square test. The trackway data alone (Analyses 123 and 126) pass the chi-square tests ($p = 1x10^{-5}$) and still support the association between wide-gauge trackways and inland environments and narrow-gauge trackways and coastal environments.

Analyses 129-134 (Table 3.9) explore the consequences of excluding both the Korean and USA trackway data (56% of the tracksite dataset). Analyses 129 and 131 (based on number of individuals) both pass the chi-square test ($p < 6x10^{-4}$: Table 3.9). Analysis 129 supports the positive association between titanosaurs/wide-gauge trackways and inland environments and non-titanosaurs/narrow-gauge trackways and coastal environments. The polarity of this association is reversed in Analysis 131; however, this is not surprising because several other analyses based on the titanosauriform/non-titanosauriform categories produce similar results (e.g. Analysis 8: Table 3.1). The three remaining locality-based analyses (nos. 132-134) all fail the chi-square tests (Table 3.9).

Analyses 135-148 – Testing each group separately

Analyses 135-148 re-investigate the first set of analyses (1-14), but consider the results of the chi-square tests for each group per environment separately (Table 3.10). The *p*-value cut off is 0.0036 as there are only 14 analyses and these are, in essence, a repeat of Analyses 1-14. Ten out of the 56 analyses produce statistically significant results. Analyses 135, 136, 145 and 146 support a positive coastal association for non-titanosaurs (135 and 136) and titanosauriforms (145 and 146). A negative association between titanosaurs and coastal environments is recovered in Analyses 135, 138, 145 and 146. Analysis 135 reveals a positive association between titanosaurs and inland environments; the opposite correlation is recovered for non-titanosaurs. Other analyses, although not statistically significant, demonstrate the same polarities in environmental preferences as these ten analyses (Table 3.10).

TABLE 3.10. Results of Analyses 135-148. Note that the *p*-values are for the four separate analyses and are listed in descending order as follows: (1) Non-titanosaurs/ titanosauriforms/ macronarians inland; (2) Non titanosaurs/ titanosauriforms/ macronarians coastal; (3) Titanosaurs/ titanosauriforms/ macronarians inland; (4) titanosaurs/ titanosauriforms/ macronarians coastal. Symbols: * Significant positive inland; ** Significant negative inland; # Significant positive coastal; ## Significant negative coastal. *P*-value cut-off is 0.0036 (*p*-value of 0.005 divided by 14 [number of analyses]).

Analysis No.	**Comparison**	**Inland**	**Coastal**	***p*-value**
135	Body fossil individuals: T = 1360	T = 1226	T = 134	0.3881
	Non-titanosaurs: T = 987	O = 864 E = 889.75	O = 123 E = 97.25	0.009# 0.1602
	Titanosaurs: T = 373	O = 362 E = 336.25	O = 11 E = 36.75	0.00002##
136	Trackway individuals: T = 633	T = 236	T = 397	< 0.00001**
	Narrow-gauge: T = 187	O = 30	O = 157	0.0002#

		E = 69.72	E = 117.28	0.0021*
	Wide-gauge: T = 446	O = 206 E = 166.28	O = 240 E = 279.72	0.0176
137	Body fossil and trackway individuals: T = 1993	T = 1462	T = 531	0.2639 0.0638
	Non-titanosaurs and narrow-gauge: T = 1174	O = 894 E = 861.21	O = 280 E = 312.79	0.1809 0.0264
	Titanosaurs and wide-gauge: T = 819	O = 568 E = 600.79	O = 251 E = 218.21	
138	Body fossil localities: T = 706	T = 624	T = 82	0.3466
	Non-titanosaurs: T = 479	O = 404 E = 423.37	O = 75 E = 55.63	0.0094 0.1808
	Titanosaurs: T = 237	O = 227 E = 209.47	O = 10 E = 27.53	0.0002##
139	Trackway localities: T = 190	T = 116	T = 74	0.0275
	Narrow-gauge: T = 41	O = 14 E = 25.03	O = 27 E = 15.97	0.0058 0.2492
	Wide-gauge: T = 150	O = 102 E = 91.58	O = 48 E = 58.42	0.1489
140	Body fossil and trackway localities: T = 896	T = 740	T = 156	0.5801 0.7033
	Non-titanosaurs and narrow-gauge: T = 520	O = 418 E = 429.46	O = 102 E = 90.54	0.5215 0.1627
	Titanosaurs and wide-gauge: T = 387	O = 329 E = 319.62	O = 58 E = 67.38	
141	Body fossil individuals: T = 1360	T = 1226	T = 134	0.8049
	Non-titanosauriforms: T = 819	O = 745 E = 738.30	O = 74 E = 80.70	0.4559 0.7616
	Titanosauriforms: T = 541	O = 481 E = 487.70	O = 60 E = 53.30	0.3588
142	Body fossil and trackway individuals: T = 1993	T = 1462	T = 531	0.1729 0.0237
	Non-titanosauriforms and narrow-gauge: T = 1006	O = 775 E = 737.97	O = 231 E = 268.03	0.1688 0.0224
	Titanosauriforms and wide-gauge: T = 987	O = 687 E = 724.03	O = 300 E = 262.97	
143	Body fossil localities: T = 706	T = 624	T = 82	0.8231
	Non-titanosauriforms: T = 370	O = 323 E = 327.03	O = 47 E = 42.97	0.8458 0.8213
	Titanosauriforms: T = 359	O = 309 E = 317.30	O = 50 E = 41.70	0.5328
144	Body fossil and trackway localities: T = 896	T = 740	T = 156	0.8933 0.7733

	Non-titanosauriforms and narrow-gauge: T = 411	O = 337 E = 339.44	O = 74 E = 71.56	0.9058 0.7958
	Titanosauriforms and wide-gauge: T = 509	O = 411 E = 420.38	O = 98 E = 88.62	
145	Body fossil individuals: T = 541	T = 481	T = 60	0.013
	Non-titanosaurian titanosauriforms: T = 168	O = 119 E = 149.37	O = 49 E= 18.63	< 0.00001# 0.0954
	Titanosaurs: T = 373	O = 362 E = 331.63	O = 11 E = 41.37	< 0.00001##
146	Body fossil localities: T = 362	T = 310	T = 52	0.0279
	Non-titanosaurian titanosauriforms: T = 122	O = 82 E = 104.48	O = 40 E = 17.52	< 0.00001# 0.1146
	Titanosaurs: T = 237	O = 227 E = 202.96	O = 10 E = 34.04	0.0001##
147	Body fossil individuals: T = 1360	T = 1225	T = 135	0.9975
	Non-macronarians: T = 565	O = 509 E = 508.92	O = 56 E = 56.08	0.992 0.9975
	Macronarians: T = 795	O = 716 E = 716.08	O = 79 E = 78.92	0.9929
148	Body fossil localities: T = 706	T = 624	T = 82	0.8395
	Non-macronarians: T = 307	O = 268 E = 271.34	O = 39 E = 35.66	0.5758 0.8695
	Macronarians: T = 467	O = 412 E = 412.76	O = 55 E = 54.24	0.6499

Discussion

Environmental associations among sauropods

Taxonomic level and polarity of the environmental association

All of the statistically significant results were obtained in analyses involving titanosaurs/non-titanosaurs, titanosauriforms/non-titanosauriforms and/or wide-gauge/narrow-gauge trackways, whereas none of the analyses involving macronarians/non-macronarians produced statistically significant results. This indicates that Butler *et al*.'s (2007) and Butler and Barrett's (2008) suggestion that macronarians are positively associated with inland habitats is probably incorrect (though note that these authors were also sceptical about the significance of their macronarian result, suggesting that it might have been generated by a taphonomic artefact). By limiting the dataset to the Cretaceous, this macronarian group is actually comprised largely of titanosauriform taxa because virtually all non-titanosauriform macronarians are Jurassic in age (e.g. *Camarasaurus*). If Butler *et al*. (2007) and Butler and Barrett (2008) had considered all sauropods rather than just Cretaceous forms, the support for the positive association between macronarians and inland environments would have been much weaker or perhaps non-existent (as was recovered here). It should be noted that the current dataset still fails to support environmental associations at the Macronaria/non-Macronaria level even when it is restricted to Cretaceous forms. This probably occurs because the current dataset is much larger: when marine deposits and indeterminate sauropod specimens are excluded, the Butler and Barrett (2008) dataset contains information on 177 Cretaceous sauropod-bearing localities, whereas the equivalent figure for the current dataset is 475.

In this study, 134 analyses have been implemented (excluding the re-investigations of the first 14: Table 3.10): of these, 93 do not produce statistically significant results; 24

support a positive association between titanosaurs, titanosauriforms and/or wide-gauge trackways and inland environments; and 17 support the opposite (i.e. negative) association. These two sets of conflicting results are examined below and are termed the 'titanosaurs prefer inland' and 'titanosaurs prefer coastal' patterns.

The results of Analyses 1-10 carry the greatest weight because they are based on the largest amount of data. Of these analyses, nos. 1-5 support the titanosaurs prefer inland habitats pattern. Four of these analyses (nos. 1, 2, 4 and 5) can be regarded as independent from each other insofar as they do not share any data in common. Only one statistically significant analysis (no. 8: body fossil and trackway individuals of non-titanosauriforms/ titanosauriforms) based on the total dataset supports the titanosaurs prefer coastal habitats pattern. It is possible that this contradiction occurs because basal titanosauriforms were positively associated with coastal environments, and a less inclusive clade (i.e. Titanosauria) subsequently switched to an inland preference. This proposal receives support from three separate lines of evidence:

- Analyses 11 and 12 partition Titanosauriformes into basal forms (non-titanosaurs) and titanosaurs. The results support positive associations between the basal forms and coastal environments and between the more derived titanosaurs and inland environments.
- Of the 103 time-sliced analyses (Tables 3.2-3.8), 14 support the titanosaurs prefer inland habitats pattern and 12 support the opposite pattern. However, 11 of these 12 contradictory analyses were generated by Middle and Late Jurassic time-slices, whereas all 14 of the results supporting the titanosaurs prefer inland habitats pattern were generated by Cretaceous time-slices. Although many of these larger-time-sliced analyses are non-independent, the stage level time-sliced analyses are effectively based on independent datasets. Of these 56 independent time-sliced analyses, 6 (all Jurassic) support the titanosaurs prefer coastal habitats pattern and 8 (all Cretaceous) support the titanosaurs prefer

inland habitats pattern. This marked division of the results along temporal lines is consistent with the view that the earliest and most basal titanosaurs (i.e. Middle-Late Jurassic forms) occurred more often than expected in coastal habitats, but the more derived Cretaceous titanosaurs displayed a preference for inland habitats.

- At least part of the support for the positive association between early and/or basal titanosaurs and coastal habitats could be an artefact generated by taxonomic problems. There are very few titanosaur body fossils from the Jurassic: the main evidence is based on *Janenschia* from the Kimmeridgian-Tithonian of Tendaguru, Tanzania. *Janenschia* has been considered to be a titanosaur by many workers (Janensch 1929; McIntosh 1990; Jacobs *et al*. 1993; Upchurch 1995; Wilson and Sereno 1998), but more recently doubt has been cast on both the titanosaurian affinities and congeneric status of the eight individuals currently assigned to this taxon (Bonaparte *et al*. 2000). Given that the dinosaur-bearing beds of Tendaguru represent coastal habitats (Aberhan *et al*. 2002), the incorrect assignment of some of the *Janenschia* individuals to the Titanosauria could have introduced noise into the dataset that would tend to obscure the titanosaurs prefer inland habitats pattern, especially for Jurassic time-slices.

Although non-significant, Analysis 3 supports the titanosaurs prefer coastal pattern, which seems counterintuitive given that Analyses 1 and 2 supported the opposite association and Analysis 3 merely represents the combination of the datasets of the first two analyses. This is an example of Simpson's Paradox, whereby a trend present in different groups is reversed when the groups are combined (Simpson 1951; Blyth 1972). This occurs when the marginal proportions are very different: in this case, the majority of body fossils are non-titanosaur (=narrow-gauge), whereas the majority of trackways are wide-gauge (=titanosaur). Although complex statistical methods exist to tease these problems apart (C. McManus pers. comm. 2010), it is perhaps best to consider it

inappropriate to combine these datasets, as the results are misleading and uninformative. This suggests that Analysis 8 was also perhaps inappropriate and that the results were uninformative.

Analyses 135-148 represent attempts to further tease apart environmental associations for each group. The results from these analyses indicate that non-titanosaurs displayed a strong negative association with inland environments and a strong positive association with coastal environments. Titanosaurs displayed a strong negative correlation with coastal environments and, in one analysis, a strong positive association with inland environments.

In summary, the results suggest that most sauropod lineages, including basal titanosauriforms and perhaps basal titanosaurs living during the Middle and Late Jurassic, displayed positive associations with coastal environments, but a more derived clade of largely Cretaceous titanosaurs developed a positive association with inland environments and a negative association with coastal settings. However, the habitat preferences of the earliest (Jurassic) titanosaurs may have been distorted or obscured by scarcity of data and taxonomic problems.

Habitat preference or sampling artefact?

A statistically significant association between an assemblage of taxa and a given environment might not, by itself, provide evidence of a genuine habitat preference. Skewed distributions can arise as a result of other factors, such as long-term trends in taxon diversity and/or abundance combined with long-term trends in the relative sampling rates of the different environmental categories. However, when analyses are run at the stage level (i.e. Analyses 30-115: Tables 3.3-3.8), statistically significant environmental associations persist, even though such analyses disrupt the effects of the long-term trend in the relative sampling of inland and coastal environments.

A further observation lends additional support to the view that the statistically significant environmental associations represent ecological preferences expressed by titanosaurs and non-titanosaurs. There are 896 trackway and body fossil localities in the dataset, but only eight of these have yielded both titanosaurs and non-titanosaurs. Three of these eight localities are Jurassic and coastal while the other five are Cretaceous and inland localities, which is consistent with the hypothesis that the earlier and more basal titanosaurs were more likely to occur in coastal environments than the Cretaceous forms. If titanosaurs and non-titanosaurs occupied all environments with no preference, it seems likely that many more localities would yield evidence for both types of sauropod living side-by-side. The relative rarity of 'shared localities' is highly suggestive of some form of genuine ecological partitioning or separation between titanosaurs and non-titanosaurs. Although the lack of shared localities in the Late Cretaceous can mainly be explained by an absence of non-titanosaurs during this epoch, this cannot explain the pattern during the Early Cretaceous (and to a lesser extent the Late Jurassic), when titanosaurs, basal titanosauriforms and diplodocoids were all abundant. Therefore, it is tentatively suggested that these results indicate evidence for habitat preferences among sauropod groups, and are not merely artefacts created by trends in the relative sampling of different environments.

Strength of the habitat preference

Inspection of the raw data and the 'observed' and 'expected' values in Tables 3.1-3.9, demonstrates that titanosaur body fossils and/or wide-gauge trackways often occur in coastal habitats, and non-titanosaur body fossils and narrow-gauge trackways often occur in inland habitats. Similar observations were made for Cretaceous herbivorous dinosaurian clades by Butler and Barrett (2008). There are two main ways in which such results might be interpreted:

The ‘weak preference hypothesis’ suggests that the occurrences of non-titanosaurs and titanosaurs across the inland and coastal environmental categories represent a largely accurate picture of sauropod distributions. Thus, the skewed environmental distributions would reflect a subtle difference between titanosaurs and non-titanosaurs, such as the relative amounts of time that members of each group spent in each environmental category, or the relative abundances of each group. If this interpretation were correct, then the difference between titanosaurs and non-titanosaurs would have been a relatively minor one; just large enough to produce a statistically detectable skew in a large dataset. Alternatively, the ‘strong preference plus noise hypothesis’ suggests that the habitat preferences of titanosaurs and non-titanosaurs were significantly different, but the strength of this signal has been reduced by ‘noise’ in the dataset. There are several possible sources of such noise, including:

- There is considerable scope for error when estimating the number of individuals based on body fossils or trackways, and determining the number of localities can also be problematic (see ‘Materials and Methods’).
- Post-mortem transport of body fossils could have carried sauropod specimens into habitats which the living animal generally avoided during life. One way to test this would be to repeat the analyses using a more stringently filtered version of the dataset, i.e. by excluding disarticulated or very incomplete specimens.
- Taxonomic and phylogenetic errors could obscure or weaken an environmental association signal. The phylogenetic relationships of basal titanosaurs and basal titanosauriforms are a relatively poorly understood part of the sauropod evolutionary tree (Upchurch *et al*. 2004a; Curry Rogers 2005); thus, the contents of the titanosaur/non-titanosaur and titanosauriform/non-titanosauriform categories could be inaccurate. Future developments in sauropod phylogenetics might result in some of the taxa classified as titanosaurs or titanosauriforms shifting in relative position, producing a strengthening or weakening of the

putative environmental associations signal (e.g. see discussion of *Janenschia*, above).

- Henderson (2006) modelled the position of the centre of mass in several sauropods and argued that all large sauropods (over 12.6 tonnes) would have been constrained to adopt a wide-gauge stance in order to maintain stability during locomotion. This would mean that many large non-titanosaurian taxa would have produced wide-gauge trackways and thus would potentially introduce errors into all of the 'combined evidence' analyses where titanosaur body fossils have been grouped with wide-gauge trackways and non-titanosaur body fossils with narrow-gauge trackways (though see above for how this 'combined evidence' approach' may be statistically inappropriate). However, many large-bodied non-titanosaurian sauropods lack most or all of the morphological modifications which Wilson and Carrano (1999) identified as adaptations for a wide-gauge stance (see also Materials and Methods). One other possibility relates to a potential link between size/mass and rock type; there might be an increased likelihood that tracks of smaller animals will be preserved in carbonates and this may lead to a bias because titanosaurs tend to be larger bodied than other sauropods. However, many non-titanosaurs are also extremely large, whereas numerous latest Cretaceous derived titanosaur taxa were small by sauropod standards (e.g. saltasaurids), yet no narrow-gauge trackways are known from this time interval. Furthermore, as noted in 'Materials and Methods', both narrow and wide-gauge tracks have been discovered alongside one another in a single, heterogeneous (coastal) environment (Day *et al*. 2002, 2004).
- The analyses are based on a simple two-fold division of habitats into inland versus coastal types. This division might partially obscure the true habitat preferences of titanosaurs and non-titanosaurs. For example, suppose titanosaurs actually preferred relatively arid conditions, and tended to occupy semi-arid inland environments: the inclusion of more mesic habitats (e.g. fluvio-

lacustrine facies) in the inland category could hide the true habitat preferences of titanosaurs. This idea may explain why titanosaurs and non-titanosaurs are rarely found at the same localities despite occurring in both coastal and inland habitat categories. It also may explain why Analyses 135-148 recovered strong negative correlations between titanosaurs and coastal environments, but a weaker signal for inland settings. An additional problem may relate to sauropod skeletons being reported in 'fluvial' (inland) environments, when the setting is actually much closer to the coastline.

Elements of both hypotheses are thus supported by the dataset and analyses. Despite the statistically significant skews in the distributions of titanosaurs and non-titanosaurs across inland and coastal environments, it is clear that both types of sauropods probably spent considerable time in both environmental categories (as demonstrated by the strong negative association between titanosaurs and coastal settings in Analyses 134-148, but the somewhat equivocal results with inland environments). However, it also seems very probable that one or more sources of noise have blurred the habitat preference signal, perhaps making it appear much more subtle than it was in reality.

Nature of the habitat preference

The 'resource exploitation hypothesis' suggests that the habitat preference is linked to particular resources in each habitat. If this hypothesis were correct, particular plant types should display non-random associations with inland and coastal habitats, and titanosaurs and non-titanosaurs should have different feeding mechanisms adapted to exploit these particular resources. However, the patchiness of our sampling of both the sauropod and plant fossil records hampers the testing of this idea. At present, relatively few titanosaurs are known from cranial material. For example, in the current sauropodomorph database there are 54 genera of titanosaurs, only 19 of which possess any cranial material. Of these 19 titanosaur genera preserving cranial material, ten are

known from isolated teeth or only the braincase, with just five known from substantial cranial material. Consequently, it is difficult to generalise about the nature of the titanosaur skull. Nevertheless, titanosaurs do seem to have possessed a number of distinctive features in both their skulls and postcrania, which can be plausibly linked to novel feeding mechanisms (Calvo 1994; Upchurch and Barrett 2000; Curry Rogers and Forster 2001; Wilson 2002, 2005a; Upchurch *et al*. 2004a; Barrett and Upchurch 2005). It is possible that features such as slender teeth restricted to the anterior ends of the jaws (at least in nemegtosaurids and *Rapetosaurus*), high-angled apical wear facets and reduced supratemporal fenestrae (Calvo 1994; Curry Rogers and Forster 2001; Wilson 2002, 2005a; Upchurch *et al*. 2004a) are related to jaw mechanisms adapted for feeding on particular plant types. Similarly, if the wide-gauge stance, increased flexibility of the dorsal vertebral column, short procoelous tails and anteriorly flaring ilia of titanosaurs are related to a tripodal stance (Borsuk-Bialynicka 1977; Powell 1992; Wilson and Carrano 1999), then such an ability may have been used during high-browsing on particular types of plant. Rothschild and Molnar (2005) cast doubt on the ability of sauropods to rear up into a tripodal stance, based on the absence of evidence for stress fractures in metacarpals and dorsal vertebrae. However, it should be noted that none of the sauropod specimens studied by these authors pertains to a titanosaur. Additionally, it seems unlikely that rearing would cause damage to an animal that actively adopted this stance, so perhaps it is unsurprising that no stress fractures have been found. A more serious challenge to the tripodal abilities of titanosaurs was made by Henderson (2006), who argued that the wide-gauge stance was related to a more anteriorly placed centre of mass (see above) which, in turn, would have made adoption of a tripodal stance more difficult in titanosaurs than in narrow-gauge sauropods such as *Diplodocus*.

One possibility is that titanosaurs were better equipped to deal with angiosperm fodder than were non-titanosaurs (except, perhaps, some diplodocoids – see below). The extinction of non-titanosaurs during the early Late Cretaceous, and the coincident diversification of titanosaurs at this time, correlates well with the ecological dominance

of angiosperms observed in the Late Cretaceous (Barrett and Willis 2001; Salgado 2001; Barrett and Upchurch 2005). The only direct evidence for titanosaurs feeding upon angiosperms comes from coprolites in Late Cretaceous deposits in India (Mohabey and Samant 2003; Mohabey 2005). These coprolites have been found in close association with titanosaur remains, and the relatively large size of the coprolites (10 cm or more in length) and their plant content also support referral to a large dinosaurian herbivore. These coprolites include the remains of several flowering plants, such as grass phytoliths and palm seeds (Ambwani and Dutta 2005; Prasad *et al*. 2005; Dutta and Ambwani 2007), but there can also be a substantial contribution from pteridophytes and gymnosperms (Ghosh *et al*. 2003; Mohabey 2005). Even if titanosaurs were adapted to deal with angiosperm fodder, the former's preference for inland environments and intolerance for coastal settings could only be explained if angiosperms could also be shown to occur preferentially in these habitats. However, no such environmental association for Cretaceous angiosperms has been proposed to date. Furthermore, the analyses of Butler *et al*. (2009b) failed to find any positive association between the geographical distributions of sauropods and angiosperms in the Cretaceous.

The 'locomotion/stance hypothesis' proposes a linkage between the wide-gauge stance of titanosaurs and some physical (perhaps topographical or substrate-related) aspect of inland environments. The adaptive significance of the wide-gauge stance is still poorly understood, though there can be little doubt that this titanosaurian feature would have had a major effect on many aspects of their locomotion and behaviour. For example, the wide-gauge stance might have increased the stability of the animal, enhancing its ability to cross uneven or sloping terrain. Wilson and Carrano (1999) noted that the wide-gauge stance is associated with several other anatomical modifications, including loss of the hyposphene-hypantrum system in dorsal vertebrae, lateral flaring of the anterior process of the ilium, increased range of motion at the knee, shortening of the tail, and development of strongly opisthocoelous and procoelous ball-and-socket joints between dorsal centra and caudal centra respectively. These authors also noted several

modifications to the shoulder girdles and forelimbs, such as the large crescentic sternal plates, robust ulna with enlarged olecranon, and increased range of motion at the elbow. All of these features suggest that titanosaurs had a wider range of motion in the trunk and tail regions and fore and hind limbs, which collectively may have enhanced their ability to rear into a tripodal stance (Wilson and Carrano 1999) and/or move more quickly (Apesteguía 2005). Thus, even if inland and coastal habitats possessed approximately the same resources, titanosaurs may have found it easier to exploit these resources in the inland habitats than did non-titanosaurs. This hypothesis could be tested by using the biomechanical approaches proposed by Henderson (2006) and Hutchinson *et al*. (2007) to model titanosaurs and non-titanosaurs walking and turning at different speeds, and rearing into a tripodal stance, on a variety of different terrains and substrates. It should be noted that nearly all of these morphological features of titanosaurs are absent in large-bodied non-titanosaurian sauropods; as discussed in 'Materials and Methods', it is difficult to find support for Henderson's (2006) proposal that body size is a better indicator of gait than taxonomy.

Sauropod evolutionary history

The diversity of non-titanosaur lineages declined through the Cretaceous, whereas, at the same time, titanosaurs radiated strongly (see also Barrett and Upchurch 2005; Upchurch and Barrett 2005). Why titanosaurs should have been so scarce during the Jurassic and so dominant in the Cretaceous (especially the Late Cretaceous) is not understood at present. In part, this pattern probably reflects sampling biases in the fossil record. It is interesting to note, for example, that titanosaurian body fossils are extremely scarce during the Jurassic (0.01% of the Jurassic part of the body fossil individual dataset), whereas wide-gauge trackways and tracksite localities make up 58% and 42% of the Jurassic track dataset, respectively. This disparity may indicate that early titanosaurs occupied environments with low preservation potentials for body fossils, and/or that some of the sauropod taxa known from the Middle and Late Jurassic might

be currently unrecognised members of the basal titanosaurian radiation. The decline of non-titanosaurs throughout the Early and early Late Cretaceous is less easily explained as a sampling artefact because there is an observable decrease in the abundance and diversity of both non-titanosaurian body fossils and narrow-gauge trackways (both are absent from the Coniacian onwards). As discussed above, the diversification of titanosaurs and decline of non-titanosaurs might be linked to the radiation of angiosperms, especially during the Late Cretaceous when these plants became a significant part of floral ecosystems (Barrett and Willis 2001; Salgado 2001; Barrett and Upchurch 2005). However, although coprolite evidence indicates that at least some titanosaurs included flowering plants within their diets (see above), there are currently too few data points to allow meaningful comparisons between titanosaurs and non-titanosaurs.

The possibility that titanosaurs exhibited a preference for inland environments and an intolerance for coastal settings (in relation to non-titanosaurs) might shed light on the titanosaurian radiation and decline of non-titanosaurs. As discussed in 'Materials and Methods', the relative number of coastal localities producing herbivorous dinosaur material decreases markedly from the Jurassic to the Cretaceous. It seems very improbable that there was a genuine decrease in the number or areal extent of coastal habitats during the Cretaceous: if anything, continental fragmentation during the Cretaceous should have increased the amount of available coastline. If the relative extent of coastal to inland habitats remained the same (or even increased) during the Cretaceous, then the observation that fewer herbivorous dinosaurs were living in coastal environments requires explanation. Titanosaurs, and perhaps certain ornithischian groups, might have been forced to occupy inland habitats more frequently during the Cretaceous because coastal environments became less hospitable (see below discussion of the 'sauropod hiatus'). If non-titanosaurs were less well equipped to deal with conditions and/or resources in the inland habitats, their dependence on coastal environments might have contributed to their decline in the Early Cretaceous.

In recent years, several authors have remarked on the convergence between diplodocoids (particularly rebbachisaurids) and titanosaurs (Upchurch 1999, p. 119-120; Curry Rogers and Forster 2004; Apesteguía 2005; Barrett and Upchurch 2005; Mannion, in review). Convergently acquired features include: narrow teeth with high-angled apical wear, a square-ended snout with teeth restricted to the extreme anterior portions, more extreme narial retraction, reduction and even closure of the supratemporal fenestra, loss of the hyposphene-hypantrum system in dorsal vertebrae, and large and crescentic sternal plates (Calvo and Salgado 1995; Upchurch 1999; Wilson 2002; Curry Rogers and Forster 2004; Upchurch *et al*. 2004a; Apesteguía 2005; Barrett and Upchurch 2005; Sereno *et al*. 2007). Rebbachisaurids seem to have diversified during the Early Cretaceous and were the last non-titanosaurian group of sauropods to go extinct. These observations hint at environmental changes during the Early and early Late Cretaceous that drove rebbachisaurids and titanosaurs to convergently acquire similar feeding and/or locomotory systems. It would be interesting to examine environmental associations for rebbachisaurids versus other non-titanosaurian sauropods, but the data available for the former is too scarce at present. However, it is worth noting that of the 25 rebbachisaurids incorporated into this analysis, only one (the putative form, *Amazonsaurus*; Carvalho *et al*. 2003) was recovered from a coastal environment, suggesting a possible 'environmental convergence' between titanosaurs and rebbachisaurids.

The mid-Cretaceous 'sauropod hiatus'

Several workers have observed that sauropod dinosaurs are absent from North American and European deposits from approximately the Cenomanian to the late Campanian inclusive (Lucas and Hunt 1989; Le Loeuff 1993; Le Loeuff and Buffetaut 1995), while they are relatively common in South America, Asia and Africa during this time interval (see reviews in Weishampel *et al*. 2004a; Salgado and Bonaparte 2007;

Wilson and Upchurch 2009; Mannion in press [a]). This absence has been coined the 'sauropod hiatus' (Lucas and Hunt 1989).

Lucas and Hunt (1989) proposed two alternative hypotheses to explain this hiatus. The first of these, the 'inland herbivore' scenario, is an attempt to explain the North American sauropod hiatus as the product of a sampling bias. Lucas and Hunt (1989) suggested the possibility that Cenomanian-Campanian sauropods have not been found because they were restricted to inland terrestrial environments in a region where the sedimentary record is almost entirely composed of coastal deposits. However, Lucas and Hunt (1989) rejected this scenario based on the lack of sauropods in the Two Medicine Formation of Montana, USA, and the Judith River Formation of Alberta, Canada (both representing terrestrial deposits of Campanian age and both rich in dinosaurs).

Their second hypothesis, the 'austral immigrant' scenario, proposed that sauropods became extinct in North America at the end of the Albian and then re-appeared during the Maastrichtian as a result of immigrations from southern continents. Lucas and Hunt (1989) provided support for this interpretation via several lines of evidence. Kues *et al*. (1980) suggested that the presence of titanosaurian sauropods throughout the Cretaceous in South America, and the formation of a land bridge between South and North America in the Campanian-Maastrichtian (Anderson and Schmidt 1983), provided support for this reinvasion scenario (see also Sloan 1970; Bonaparte 1984; Lehman 1987). Furthermore, Lucas and Hunt (1989) argued that *Alamosaurus* (the only currently known Late Cretaceous taxon from North America) was a close relative of South American titanosaurs, providing further evidence for a Gondwanan reinvasion in the Maastrichtian. Kues *et al*. (1980) and Lucas and Hunt (1989) also posited that the North American sauropod extinction might have been related to a late Albian marine regression (Kauffman 1984), while Buffetaut (1989) suggested the possibility of competitive replacement by ornithischian dinosaurs.

As mentioned above, other authors have commented on a similar sauropod hiatus in Europe between the late Cenomanian and late Campanian (i.e. Le Loeuff 1993; Le Loeuff and Buffetaut 1995) and attempted to explain it in similar terms as Lucas and Hunt's (1989) 'austral immigrant' scenario. Le Loeuff and Buffetaut (1995, p. 183) wrote: 'The Early Campanian faunas are remarkable because of the absence of titanosaurid dinosaurs, which are the dominant herbivorous dinosaurs in the Late Campanian and Early Maastrichtian. This can suggest a post-Cenomanian extinction of this group in Europe followed by a late Campanian immigration', while Le Loeuff (1993, p. 112) commented: 'They would have reached Europe again, probably from Africa, during the Late Campanian'. Buffetaut (1989, p. 70) also considered an austral immigration likely, writing: 'the occurrence and abundance of titanosaurid sauropods in the Maastrichtian land faunas of Europe can definitely be interpreted as indicating Gondwanan affinities'. However, Le Loeuff (1993, p. 112) cautioned that the richest early Campanian European non-marine localities were deposited in estuarine environments and warned that 'a paleoecological bias is not unlikely, titanosaurids being probably more continental animals'.

In recent years the 'austral immigrant' hypothesis, and indeed the idea of a mid-Cretaceous sauropod extinction in North America and Europe, has been challenged by a number of new discoveries and analyses, which are outlined and discussed below.

New discoveries

New fossil discoveries have considerably shortened the length of the proposed hiatus (Fig. 3.1). Sauropod specimens have been recovered from the Cenomanian of the USA, including indeterminate sauropod teeth from the Mussentuchit Member of the Cedar Mountain Formation, Utah (Maxwell and Cifelli 2000), an undescribed titanosauriform forelimb from the Dakota Formation (K. Carpenter pers. comm. 2008), and a

brachiosaurid (originally described as *Sonorasaurus*; Ratkevich 1998) from the Turney Ranch Formation (late Albian-early Cenomanian), Arizona (Fig. 3.1B). These occurrences suggest that any North American extinction was not caused by a late Albian marine regression. In addition, late Campanian sauropod material from North America is now known, including a titanosaurian caudal vertebra from Arizona (McCord 1997), material referred to *Alamosaurus* from New Mexico (Lucas and Sullivan 2000; Sullivan and Lucas 2000) (though see Williamson and Weil [2008] who argued that this is from no earlier than the Campanian/Maastrichtian boundary) and titanosaurian remains from northern Mexico (Benammi and Montellano-Ballesteros 2006). Thus, Lucas and Hunt's (1989) rejection of the 'inland herbivore' scenario can be criticised on two grounds: (1) titanosaurs are now known to have been present in North America during the late Campanian; and (2) climatic regime or ecological barriers might have been responsible for the absence of sauropods in the more northerly Judith River region (also see Butler *et al*. [2009a, fig. 4] for a visual representation of the distribution of latest Cretaceous sauropods in North America).

Furthermore, Mezga *et al*. (2006) described late Turonian-early Coniacian 'wide-gauge' sauropod tracks (lacking manual claw impressions), from the island of Hvar in central Dalmatia, Croatia (Fig. 3.1B), with derived titanosaurs the most likely candidates for producing such tracks (see Wilson and Carrano 1999; Day *et al*. 2004). Thus, the hiatus has been cut to the Turonian-early Campanian in North America, and in Europe it is reduced to two short periods of absence in the late Cenomanian-early Turonian and late Coniacian-Santonian (as also commented upon by Company Rodríguez *et al*. 2009).

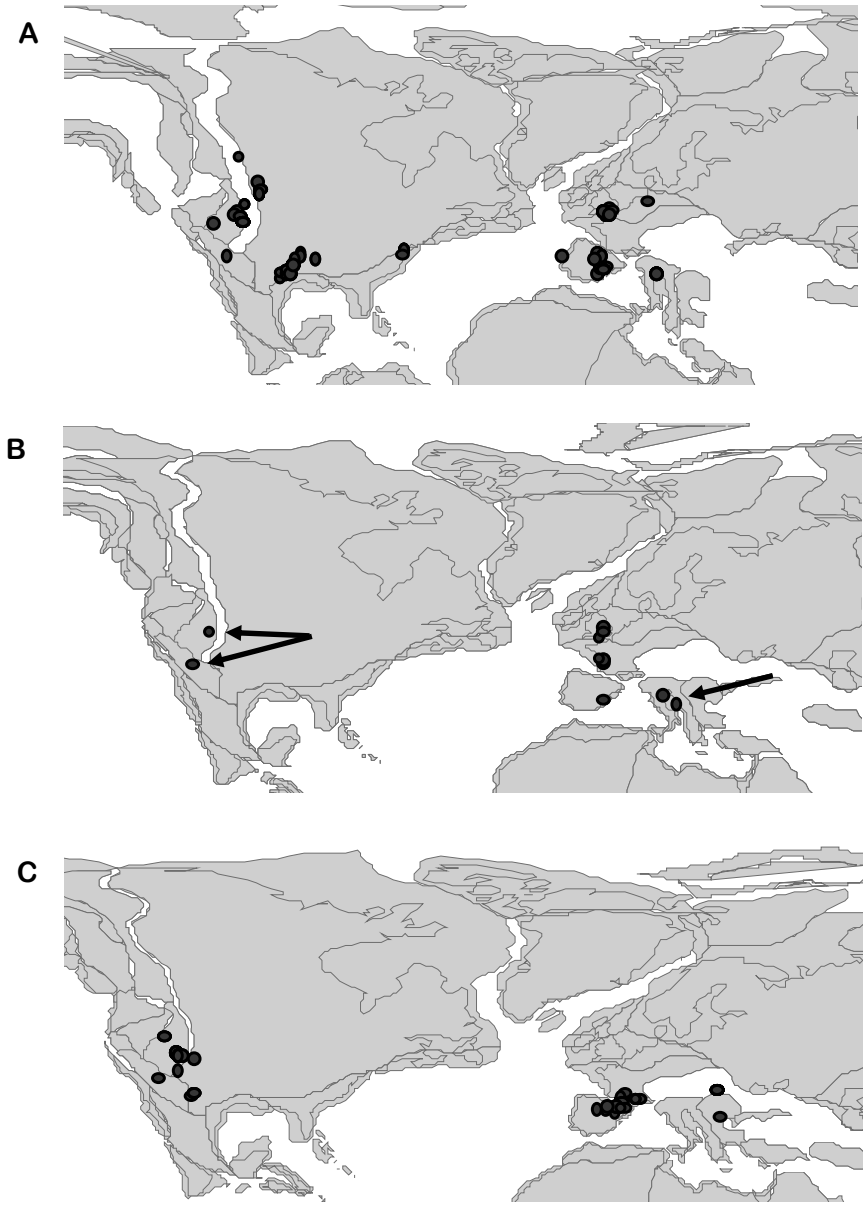

FIGURE 3.1. Palaeomaps of North America and Europe in the Cretaceous, showing sauropod occurrences (body fossils and tracksites): (A) Early Cretaceous (Berriasian-Albian); (B) mid-Late Cretaceous (Cenomanian-early Campanian); (C) Late Cretaceous (late Campanian-Maastrichtian). Particular attention should be drawn to the late Turonian-early Coniacian trackways in coastal deposits in Croatia and the Cenomanian body fossils in N. America (both highlighted with an arrow on Map B). Images produced in ArcGIS and palaeomap reconstructions from Scotese (2001). Note that the palaeomaps consist of the reconstructed positions of present-day continental coastlines.

Palaeoenvironmental support

The above analyses of the environmental associations of sauropods have provided evidence for a titanosaurian preference towards inland habitats. These results suggest that the 'inland herbivore' hypothesis of Lucas and Hunt (1989) provides a better explanation for the scarcity of sauropods in the early Late Cretaceous of North America and Europe than does the 'austral immigrant' scenario. If titanosaurs preferred inland environments, then time periods when a region's sedimentary record is dominated by coastal deposits are much less likely to preserve their remains. Earlier in sauropod evolution, such a sampling bias would have been less noticeable because of the higher probability of finding non-titanosaurs in coastal deposits. However, post-Albian non-titanosaurs are very rare (10% and 12% of post-Albian body fossil individuals and localities, respectively), so any region dominated by coastal deposits has a decreased probability of preserving any sauropod remains. Coastal deposits constitute a significant proportion of the Cenomanian-Campanian records of North America and Europe: of 71 named dinosaur-bearing formations (Carrano 2008b; www.paleodb.org), 48% can be categorized as 'coastal' or 'shallow marine'. Furthermore, the sedimentary rock outcrop areas for western Europe estimated by Smith and McGowan (2007) indicate that the preservation of terrestrial deposits increased from the Late Jurassic to Barremian, declined through the Aptian-Albian, was particularly low during the Cenomanian to Coniacian, and then rose to a peak again in the Maastrichtian (Fig. 3.2). This pattern of terrestrial sediment deposition/preservation correlates well with the abundance of titanosaurs during the Early and latest Cretaceous and their apparent absence during the early Late Cretaceous, suggesting that the mid-Cretaceous 'hiatus' is most plausibly interpreted as a sampling bias related to the dominance of coastal sediments preserved in these regions.

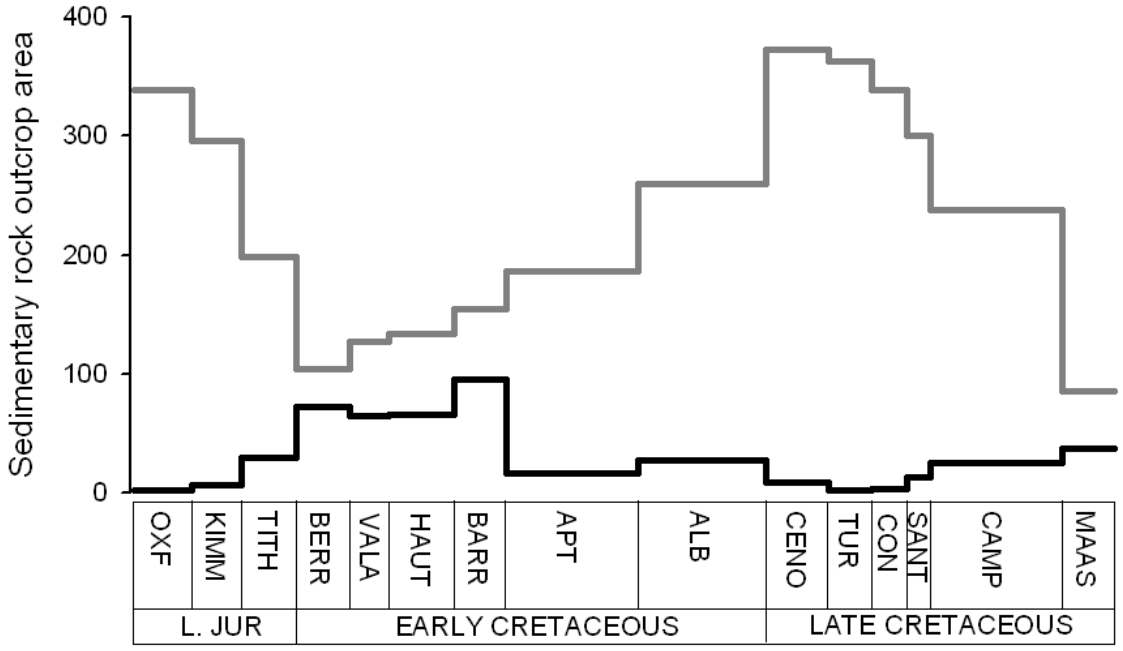

FIGURE 3.2. Terrestrial (black line) and marine (grey line) sedimentary rock outcrop areas for Western Europe for the Late Jurassic and Cretaceous (modified from Smith and McGowan 2007).

Additionally, Lehman (2001, p. 321) noted that *Alamosaurus* was an apparent inhabitant of 'upland' (i.e. inland) environments and argued that: 'Unlike coastal species, inhabitants of upland regions tend to be more endemic and less capable of dispersal over stretches of open water', suggesting that an immigration scenario was unlikely. Lehman (2001) proposed the 'descent from the highlands' hypothesis, in which he suggested that rising sea levels in the Late Cretaceous of North America may have resulted in isolation of upland faunas (including titanosaurs), while ceratopsians and hadrosaurids were better adapted to coastal environments (although note that while Butler and Barrett [2008] found statistical support for a positive association between hadrosaurids and marine environments, they found a positive correlation between ceratopsians and terrestrial environments). Lehman (2001, p. 322) then posited that the return of upland faunas might 'simply record a shifting of existing species to lower

elevations as altitudinal life zones expanded with the regression of the interior epeiric sea', with these upland faunas having 'largely escaped the reach of the fossil record, persisting ultimately to descend into nearby inland areas' and perhaps later encroaching into 'lower altitudes as the climate in the western interior became increasingly dry and continental'. The conclusions based on the palaeoenvironmental analyses provide support for Lehman's (2001) hypothesis.

Phylogenetic and biogeographic evidence

The basis for proposing that *Alamosaurus* and Late Cretaceous European titanosaurs (i.e. *Magyarosaurus*, *Lirainosaurus* and *Ampelosaurus*) are nested within Gondwanan titanosaurian clades is not well supported. Wilson and Sereno (1998) noted that *Alamosaurus* is potentially the sister-taxon to the Late Cretaceous Asian titanosaur *Opisthocoelicaudia* (see also the phylogenies in Wilson 2002; Upchurch *et al*. 2004a and Curry Rogers 2005). Similarly, Late Cretaceous European titanosaurs have been shown to be closely related to African and Asian forms (Curry Rogers 2005). Thus, if sauropods re-invaded North America and Europe during the latest Cretaceous, the sources of the new taxa could have included Gondwanan areas such as Africa and South America, but also Asia (Wilson and Sereno 1998; Wilson and Upchurch 2003).

The 'austral immigrant' hypothesis is related to the long-standing view that titanosaurs represent a southern hemisphere (Gondwanan) radiation (e.g. Bonaparte and Kielan-Jaworowska 1987; Lucas and Hunt 1989). This belief arose in the first half of the 20th Century because many of the earliest discoveries of titanosaur remains were made in South America, India and Madagascar, whereas titanosaur fossils were virtually non-existent in Northern continents (Lydekker 1877, 1893; Depéret 1896; Huene 1929, Huene and Matley 1933; Wilson and Upchurch 2003). However, a Gondwanan origin for titanosaurs has been undermined by the discovery that the earliest known evidence for titanosaurs are wide-gauge trackways from the Middle Jurassic of Portugal and England

(Santos *et al*. 1994; Day *et al*. 2002; 2004), and it is also clear that titanosaurs were globally distributed by at least the Early Cretaceous (Wilson and Upchurch 2003, 2009, and references therein). These discoveries, as well as area relationships reconstructed by cladistic biogeographic analyses (Upchurch *et al*. 2002), suggest that titanosaurs originated during or before the Middle Jurassic, and acquired a global distribution at a time when most or all portions of Pangaea were still in contact. Thus, it is conceivable that the titanosaurs in the latest Cretaceous of North America and Europe were descendants of other northern hemisphere titanosaur lineages present in these areas in the Early Cretaceous, as also suggested by Lehman (2001, p. 321), who commented: '...it is just as likely that the immediate ancestor of *Alamosaurus* was an indigenous inhabitant of North America'.

Wider implications – methodological issues

Body fossils compared with trackways

Whereas body fossils can be transported to different environments after the death of an organism, trackways provide a direct record of where the animal actually stood while alive (Thulborn 1982; Lockley 1991; Wilson and Carrano 1999; Carrano and Wilson 2001). However, there are two ways in which the information content of trackways is limited in comparison to that of body fossils. First, there are considerably more body fossils described for sauropods than there are trackways. For example, in the dataset utilised in this study, there are 706 and 190 localities that yield sauropod body fossils and trackways respectively. Second, many body fossils can be assigned to distinct clades and/or to particular genera and species. These analyses provide an opportunity to compare the relative performances of trackway-based and body fossil-based datasets.

If post-mortem transport of body fossils has had a strong masking effect on habitat preferences, then it would be expected that the analyses based solely on trackway data

would provide stronger support for environmental associations than those based just on body fossils. However, a survey of Tables 3.1-3.9 reveals both body fossil data (13 analyses) and trackway data (14 analyses) yield statistically significant results, and there is no general trend towards trackway data producing lower *p*-values than body fossil data. These comparisons do not support the argument that the body fossil data displays a weaker signal in favour of environmental associations relative to the trackway data (see similar results in Chapter 6).

Localities versus individuals

Although the definition of a 'locality' is perhaps more arbitrary than the definition of an 'individual', the initial expectation was that numbers of individuals would provide a less reliable guide to environmental associations, based on the assumption that estimation of the number of individuals (including fragmentary remains of vertebrate skeletons or numbers of trackways) is likely to result in significant errors. However, the analyses suggest that, if anything, individual-based analyses are more likely to find evidence for environmental associations than are locality-based ones. This phenomenon may be related to the fact that the number of individuals cannot be less than, and will often exceed, the number of localities. If the skew in the spatial distributions of the two taxon categories is relatively subtle, then this skew will be more easily detected in individual-based analyses because of the larger number of data points. It is possible that a habitat preference might be expressed in terms of how much time each taxon spends in a given habitat, or the relative abundances of these taxa in each habitat. Locality-based estimates of occurrences cannot capture this information very effectively because, once a taxon has been found at a locality, the number of occurrences does not increase even if other members of that taxon are discovered there. Thus, individual-based counts of occurrences may play a useful role in capturing aspects of palaeoecology that are ignored by locality-based counts, even for groups such as vertebrates and plants where the estimation of the numbers of individuals is prone to significant error. This has

parallels with modern ecological studies attempting to assess population size, where total counts are often impractical as a consequence of time, costs and size of area (Waite 2000). Consequently, population size must be estimated using alternative techniques such as sample counts or capture-mark-recapture methods (Burnham and Overton 1979; Blower et al. 1981; Chao 1987; Waite 2000), using a variety of statistical approaches (see Colwell and Coddington 1994; Krebs 1999; Waite 2000; Sutherland 2006). Some of these analytical methods have also been implemented in palaeoecological analyses (e.g. Harrington and Jaramillo 2007), but have yet to be applied to fossil vertebrates, and represent avenues for future research.

The costs and benefits of time-slicing and sensitivity analyses

As discussed earlier, it cannot be known, *a priori*, how many signals are present within a large complex dataset, how these signals conflict with each other, and how they are distorted with regard to taxonomic group or temporal range. Exploring the dataset using a wide range of different subsets of the data can ameliorate these difficulties. One of the most useful approaches is to time-slice the data in order to disrupt long-term diversity and environmental preservation trends (see also discussion in Chapter 4). One insight that can emerge from such studies is that putative environmental associations have changed through time. There is, however, one key disadvantage associated with time-slicing the dataset: as time-slices become narrower, they include fewer data points. This may result in numerous analyses that fail to find any statistically significant results, even though the dataset as a whole contains such signals (see Tables 3.2-3.8 for examples). Time-slicing is a key tool in the search for environmental associations because it allows the researcher to explore the dataset and 'fine-tune' the temporal range and taxonomic level of the proposed signals. However, time-slicing should be applied with caution because it can produce misleading inferences of the taxonomic level of a proposed environmental association (e.g. Cretaceous 'Macronaria' has virtually the same taxonomic content as 'Titanosauriformes').

In this study, limited 'jack-knifing' of the data was carried out. The results of these revised analyses demonstrate that conclusions regarding environmental associations are affected by the presence/absence of these data blocks, although several analyses continue to support the general inference that titanosaurs displayed a positive association with inland habitats (Table 3.9). Uneven sampling of the fossil record is a topic of major concern at present, particularly with regard to the temporal distributions of fossil taxa and the reconstruction of diversity curves (see Chapter 4). The impact of uneven sampling on analyses of the spatial distribution of taxa has received considerably less attention (though see Chapter 6), despite the probability that the ambiguity of 'absence' has an important impact on both palaeobiogeographic and palaeoecological analyses (Ronquist 1997; Lieberman 2000; Hunn and Upchurch 2001; Upchurch and Hunn 2002).

CHAPTER FOUR

DIVERSITY

Parts of this chapter form the basis for the following paper:

Mannion, P. D., Upchurch, P., Carrano, M. T. and Barrett, P. M. 2010. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews*, doi: 10.1111/j.1469-185X.2010.00139.x

Analyses and Results

In this section the results of the various analyses implemented are outlined and presented, beginning with a description of the updated TDE. The comparisons between the different PDEs are also reported, as are the statistical tests between diversity (both TDE and PDE) and sampling proxies. Lastly, the statistical comparisons between the 'corrected' diversity curves and sea level are presented.

One issue concerns the choice of time bins, as stages vary in duration. Rarefaction is time-dependent, so more taxa might be sampled during longer time periods; thus, it is perhaps best to use time bins of approximately equal duration (Raup 1975; Alroy *et al*. 2001, 2008). Also, more genera might have been present during longer time intervals than short ones, even when both had similar levels of diversity at any one point in time. Additionally, there may be a higher chance of genera being preserved given a longer time period. For example, the Early Cretaceous is 45.9 Myr while the Late Jurassic is only 15.7 Myr in duration. Similarly, the Campanian represents a time interval of 12.9 Myr while the Hettangian is only 3.1 Myr in duration. However, when TDE and length of stage and epoch are compared, there are no statistically significant correlations ($p > 0.3$ for all tests). In addition, there is no correlation between time bin duration and number of samples ($p > 0.1$ for all tests). Consequently, the choice of time bins seems adequate for these analyses.

Sauropodomorph taxic diversity

The updated taxic diversity curve (Fig. 4.1) largely follows previous analyses (i.e. Barrett and Upchurch 2005; Upchurch and Barrett 2005; Barrett *et al*. 2009) and so only two slight differences will be commented on. Firstly, a diversity trough in the Oxfordian was demonstrated by both Upchurch and Barrett (2005) and Barrett *et al*. (2009), and the new TDE agrees with this, but indicates that this represents the nadir in

sauropodomorph diversity. Secondly, the TDE shows an early Maastrichtian increase in diversity from the Campanian, with the peak close to that of the Kimmeridgian–Tithonian apex (Fig. 4.1). Such a substantial peak has not been reported in previous sauropodomorph diversity analyses (although notable peaks are still apparent in Upchurch and Barrett [2005] and Barrett *et al*. [2009]) and reflects the large number of taxa named from the latest Cretaceous in recent years (e.g. *Maxakalisaurus* and *Uberabatitan*), following the publication of these earlier diversity analyses.

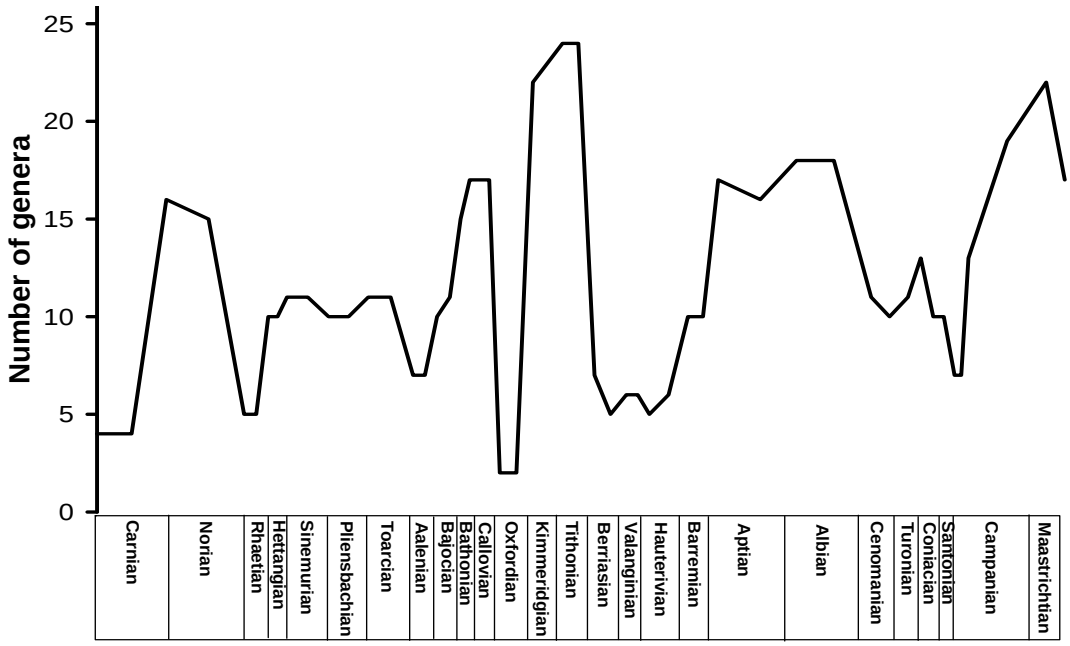

FIGURE 4.1. Taxic diversity curve (TDE) for the Sauropodomorpha through time. This graph (and all subsequent graphs) is plotted at the substage level; i.e., the early Carnian data point is plotted at the beginning of the Carnian stage, the late Carnian data point is plotted at the midpoint of the Carnian stage and the early Norian data point is plotted at the beginning of the Norian stage, etc.

Statistical comparisons between phylogenetic and taxic diversity

A diversity curve based on a composite cladogram of Upchurch *et al*. (2004a, 2007a) [UPDE] has been compared with curves derived from the basal sauropodomorph and sauropod diversity curves of Yates (2007) [YPDE] and Wilson (2002) [WPDE], respectively. Comparisons have also been made between UPDE and taxic diversity [TDE], as well as the sauropodomorph element of the supertree of Lloyd *et al*. (2008) [LPDE], in an attempt to elucidate sauropodomorph diversity. Lastly, UPDE and TDE have also been compared with the diversity curves of Barrett *et al*. (2009) [BTDE and BPDE]. To make comparisons more meaningful, only the basal sauropodomorph element of the UPDE (i.e. Upchurch *et al*. 2007a) has been compared with YPDE; similarly, only the sauropod element of the UPDE (i.e. Upchurch *et al*. 2004a) has been compared with WPDE. Figure 4.2 displays the UPDE, LPDE, YPDE and WPDE curves, while Table 4.1 reports the statistical comparisons.

TABLE 4.1. Results of statistical analyses comparing the various diversity curves to one another. See Figure 4.2 for an explanation of the abbreviations of diversity curves. When the time-interval is not stated, this means that the analysis was run for the Late Triassic-Cretaceous. LT = Late Triassic, J = Jurassic, EJ = Early Jurassic, K = Cretaceous, EK = Early Cretaceous, LK = Late Cretaceous, Bar = Barremian, Maa = Maastrichtian.

Comparisons	**Spearman's rs**	**Kendall's tau**
UPDE vs. YPDE (LT-J)	0.875 (p<0.001)	0.758 (p<0.001)
UPDE vs. WPDE (J-K)	0.637 (p<0.001)	0.515 (p<0.001)
UPDE vs. TDE	0.321 (p=0.009)	0.260 (p=0.006)
UPDE vs. TDE (LT-J)	0.877 (p<0.001)	0.730 (p<0.001)
UPDE vs. TDE (K)	-0.373 (p=0.067)	-0.286 (p=0.077)
UPDE vs. TDE (Bar-Maa)	0.301 (p=0.228)	0.233 (p=0.258)
TDE vs. BTDE	0.812 (p<0.001)	0.667 (p<0.001)
UPDE vs. BTDE	0.499 (p=0.001)	0.404 (p=0.001)
UPDE vs. BPDE	0.839 (p<0.001)	0.698 (p<0.001)

TDE vs. BPDE	0.264 (p=0.073)	0.198 (p=0.064)
UPDE vs. LPDE	0.444 (p=0.001)	0.331 (p<0.001)
TDE vs. LPDE	0.358 (p=0.013)	0.260 (p=0.014)

Overall, UPDE and YPDE are strongly correlated with one another, while UPDE and WPDE show a moderately strong correlation (see Table 4.1). The correlation between UPDE and TDE is considerably weaker, although when restricted to just the Late Triassic–Jurassic, this correlation is extremely strong (while there is no correlation between the two curves for the Cretaceous; Table 4.1). UPDE and TDE are strongly correlated with BPDE and BTDE, respectively, but show no, or only a very weak, correlation when the phylogenetic and taxic diversity estimates are compared (Table 4.1). Lastly UPDE and TDE show only a weak correlation with LPDE.

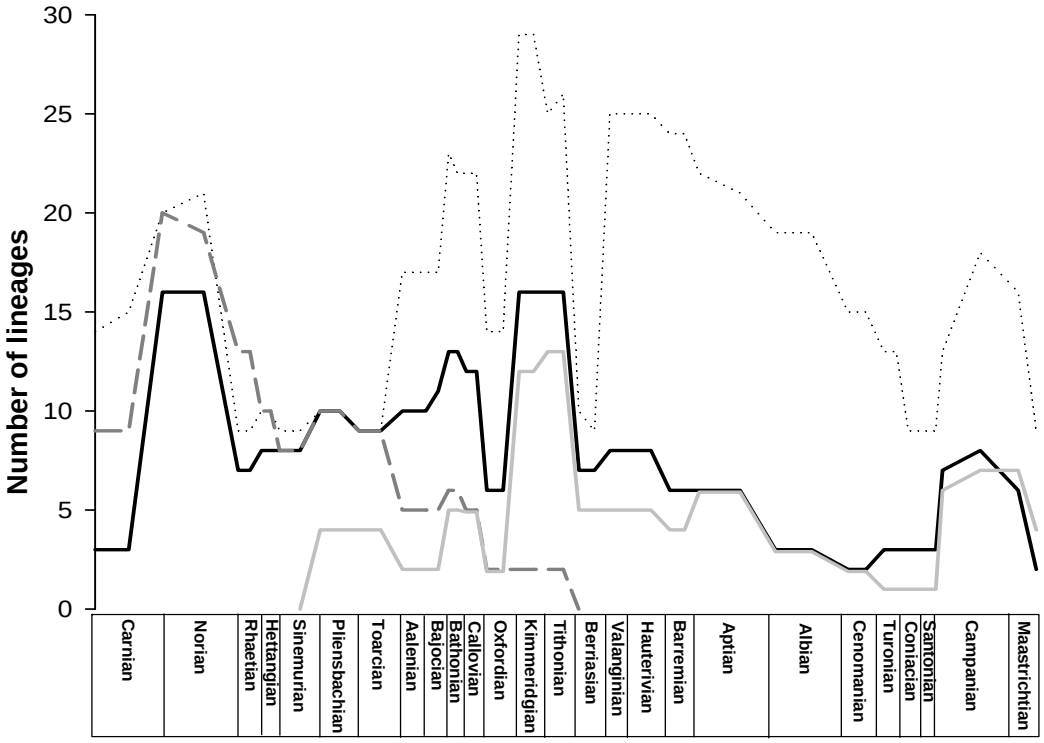

FIGURE 4.2. Comparison of the four phylogenetic diversity estimates (PDEs) through time: Wilson (2002) [WPDE] = solid grey line; Upchurch *et al*. (2004, 2007) [UPDE] = solid

black line; Yates (2007) [YPDE] = dashed grey line; Lloyd *et al*. (2008) [LPDE] = dotted black line.

Statistical comparisons between diversity and sampling proxies

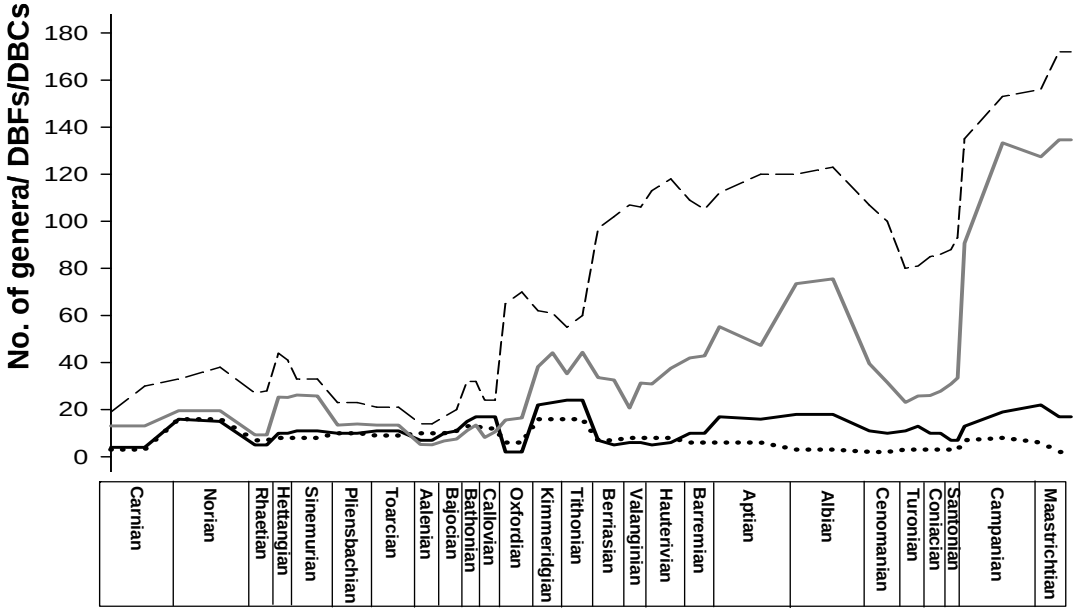

FIGURE 4.3. Taxic diversity (TDE [black solid line]) and phylogenetic diversity estimate based on Upchurch *et al*. (2004, 2007; UPDE [black dotted line]) compared with dinosaur-bearing formations (DBFs [black dashed line]) and dinosaur-bearing collections (DBCs [grey solid line]) through time. Note that DBCs have been divided by 10 to allow the curves to be plotted together.

UPDE and TDE have been compared with numbers of DBFs and DBCs (Fig. 4.3), as well as western European rock outcrop (Fig. 4.4). Overall, there is a negative correlation between DBFs and the UPDE, but no significant correlation with the TDE (see Table 4.2). Barrett *et al*. (2009) also found only a weak correlation between sauropodomorph genus richness and DBFs and commented (p. 2671) that 'the latter measure is an exceptionally poor predictor of sauropodomorph diversity'. There is no correlation between the UPDE and DBFs when smaller time bins (period and epoch) are considered,

with the exception of a moderately strong, negative correlation in the Early Jurassic (Table 4.2). The number of DBCs is positively correlated with the TDE for the Mesozoic and has a weakly negative correlation with the UPDE (Table 4.2). A correlation exists between DBCs and TDE for the Late Triassic–Early Jurassic, while the TDE (but not the UPDE) shows a significant correlation with both DBFs and DBCs when only the Cretaceous is considered (Table 4.2).

TABLE 4.2. Results of statistical analyses comparing diversity with preservational and sampling proxies. See Table 4.1 for an explanation of the abbreviations of diversity curves and proxies and Figure 4.2 and the text for other abbreviations.

Comparisons	**Spearman's rs**	**Kendall's tau**
UPDE vs. DBFs	-0.526 (p<0.001)	-0.334 (p=0.001)
UPDE vs. DBFs (LT-EJ)	0.112 (p=0.717)	0.121 (p=0.610)
UPDE vs. DBFs (EJ)	-0.733 (p=0.048)	-0.537 (p=0.100)
TDE vs. DBFs	0.174 (p=0.221)	0.114 (p=0.257)
TDE vs. DBFs (LT-EJ)	0.290 (p=0.333)	0.160 (p=0.498)
TDE vs. DBFs (K)	0.490 (p=0.020)	0.314 (p=0.043)
UPDE vs. DBCs	-0.355 (p=0.013)	-0.260 (p=0.011)
TDE vs. DBCs	0.427 (p=0.002)	0.272 (p=0.008)
TDE vs. DBCs (LT-EJ)	0.636 (p=0.018)	0.470 (p=0.036)
TDE vs. DBCs (K)	0.663 (p<0.001)	0.491 (p<0.001)
TDE_{WE} vs. terrestrial rock	0.617 (p<0.001)	0.501 (p<0.001)
TDE_{WE} vs. marine rock	-0.555 (p<0.001)	-0.445 (p<0.001)
TDE_{WE} vs. TDE	0.119 (p=0.381)	0.095 (p=0.377)
TDE_{WE} vs. UPDE	0.411 (p=0.006)	0.332 (p=0.005)

There is no correlation between either the TDE or UPDE and terrestrial western European rock outcrop area (Fig. 4.4; Table 4.2). Furthermore, there is no correlation

when diversity and marine rock outcrop are compared (Table 4.2). However, when only western European taxic diversity (TDE_{WE}) is considered, there is a relatively strong correlation with both terrestrial (positive) and marine (negative) rock area (see Table 4.2). TDE_{WE} shows no correlation with global TDE but, slightly surprisingly, is correlated with the UPDE.

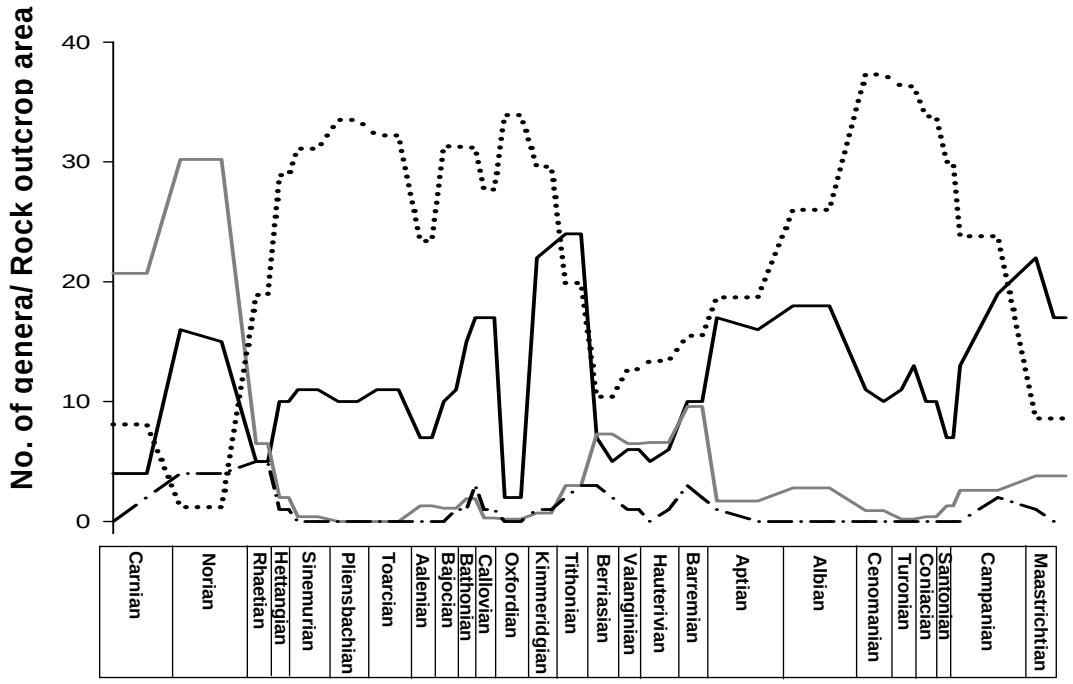

FIGURE 4.4. Global taxic diversity (TDE [black solid line]) and western European taxic diversity (TDE_{WE} [black dash-dot line]) compared with western European rock outcrop area (Smith and McGowan 2007): terrestrial rock (solid grey line) and marine rock (black dotted line) through time. Note that the rock outcrop values have been divided by 10 to allow the curves to be plotted together.

Residuals and Rarefaction

As noted in 'Materials and Methods', residuals have been implemented only for those proxies correlated with diversity (and only for the particular time-intervals they are

correlated with). Following the previous section, TDE-based residuals were thus constructed for DBCs throughout the Mesozoic, as well as for Cretaceous DBFs (Fig. 4.5). PDE-based residuals were constructed only for Early Jurassic DBFs. The residual peaks and troughs are shown in Figure 4.5 and described in the Discussion.

Implementation of 'generic-only' rarefaction allows only a few observations to be made regarding fluctuations in diversity, because of sizable error bars (Fig. 4.6A). Similar problems affect 'all-occurrences' rarefaction; however, much more is discernible from these diversity plots (Fig. 4.6B-D). Those peaks and troughs that can be distinguished are commented upon in the Discussion.

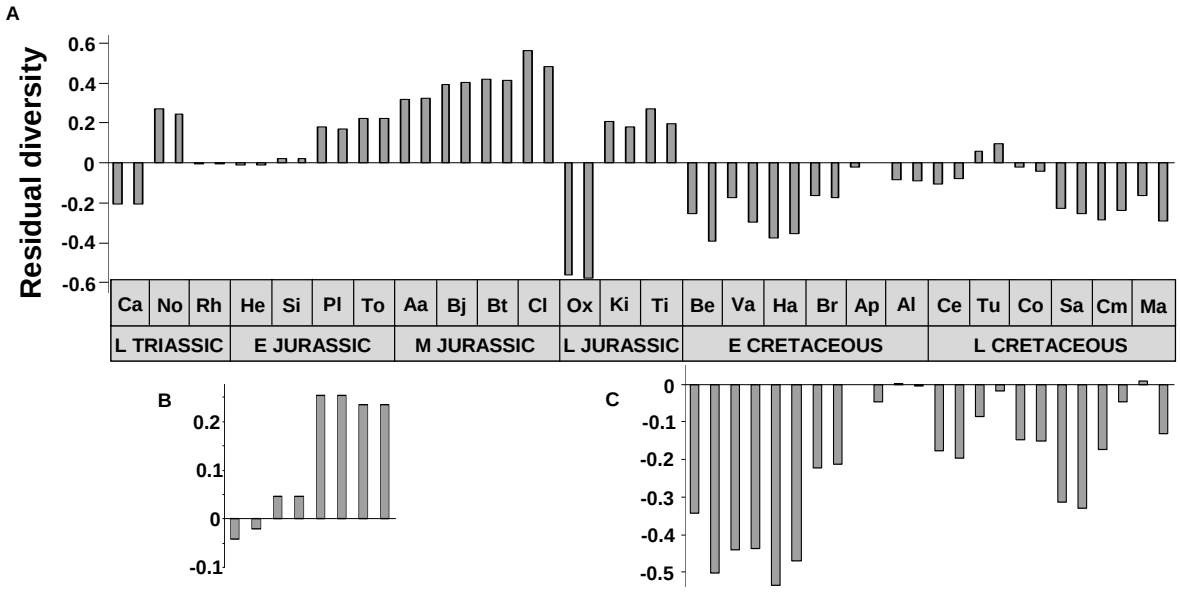

FIGURE 4.5. Residual diversity through time: (A) TDE-based residuals using DBCs for the Mesozoic; (B) UPDE-based residuals using DBFs for the Early Jurassic; (C) TDE-based residuals using DBFs for the Cretaceous. See 'Materials and Methods' for more details.

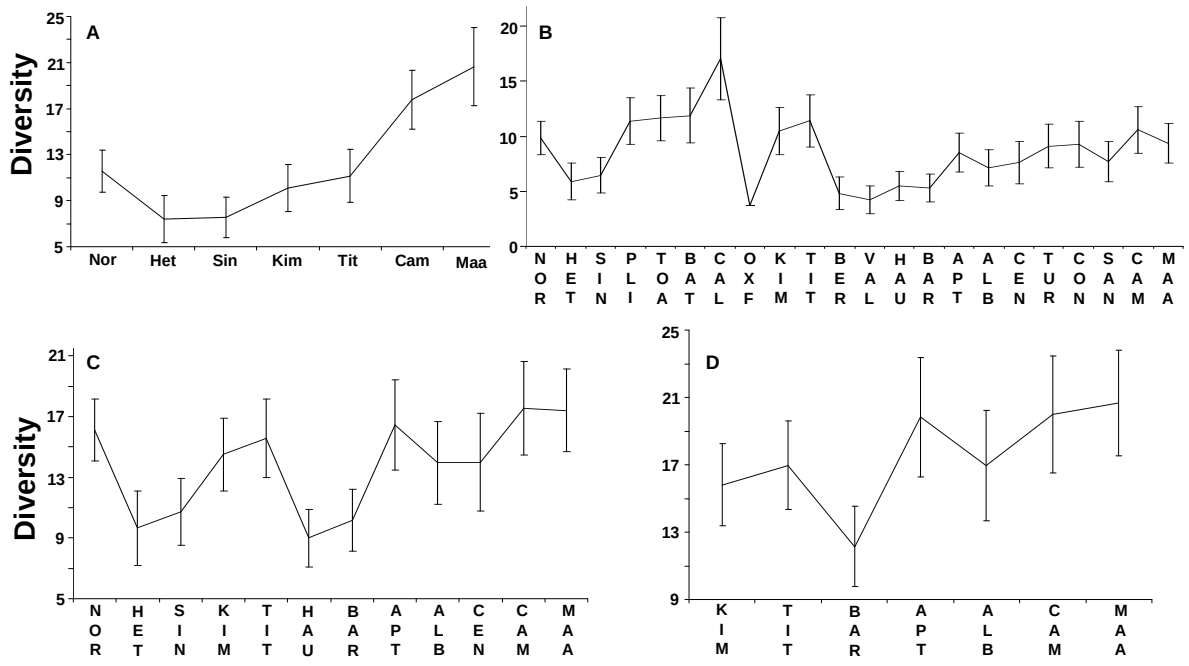

FIGURE 4.6. Rarefied diversity through time: (A) Generic occurrences only (sample size = 30); (B) All-occurrences (sample size = 30); (C) All-occurrences (sample size = 70); All-occurrences (sample size = 89). See 'Materials and Methods' for more details.

Historical collecting effort

In total, 175 sauropodomorph taxa are considered valid in this study (see 'Materials and Methods'). Their cumulative rate of discovery displays no asymptote and is in the rapid increase phase (Benton, 1998; see Chapter 5: fig. 5.3), suggesting that many more genera remain to be discovered (Wang and Dodson 2006). New discoveries are not driving back the geological age of the oldest sauropodomorphs (e.g. *Thecodontosaurus*, from the late Carnian–Rhaetian of the UK, was the first sauropodomorph to be scientifically described [Riley and Stutchbury 1836] and still remains one of the oldest known), nor are they extending our knowledge into younger time periods (e.g. *Magyarosaurus* from the late Maastrichtian of Romania was described by Nopcsa [1915], but no Paleogene sauropods have been recovered subsequently). However, new discoveries are filling many gaps in the sauropod fossil record, e.g. *Bonitasaura* and

Futalognkosaurus have been named in recent years from the early Late Cretaceous, an interval which previously has yielded very little sauropod material.

Of these 175 valid taxa, 50 come from Asia and 46 from South America. 30 taxa have been described from Europe, 25 from Africa, and 21 from North America; just 2 have been described from Australasia and only 1 from Antarctica. Three countries account for over half of all sauropodomorph diversity: Argentina (38 taxa), China (36 taxa) and the USA (20 taxa). Over half (101 genera) of sauropodomorph taxa are from Laurasia, with 74 from the approximately equally sized Gondwana (Smith *et al*. 1994). Given their similarity in surface area, this distributional skew almost certainly reflects the Northern Hemisphere origin of dinosaur palaeontology: of note is that just two Gondwanan taxa were named prior to the 1910s, compared to 20 Laurasian taxa.

Comparisons between sea level and 'corrected' diversity

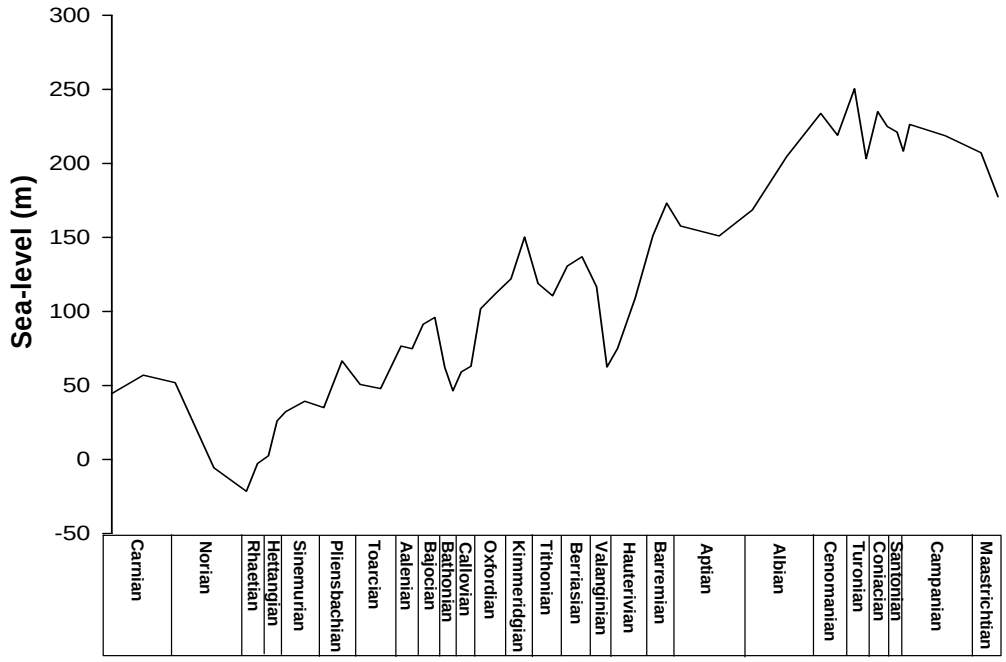

FIGURE 4.7. Mesozoic sea level curve (Haq *et al*. 1987). See text for discussion of correlations with 'corrected' diversity.

TABLE 4.3. Results of statistical analyses comparing 'corrected' diversity with sea level. See Table 4.1 for an explanation of the abbreviations of diversity curves and proxies and Figure 4.2 for other abbreviations. Haq = Haq *et al*. (1987), Miller = Miller *et al*. (2005).

Comparisons	Spearman's rs	Kendall's tau
UPDE vs. Haq sea level	-0.561 (p<0.001)	-0.397 (p<0.001)
UPDE vs. Haq sea level (J)	0.479 (p=0.023)	0.381 (p=0.011)
UPDE vs. Haq sea level (K)	-0.657 (p<0.001)	-0.549 (p<0.001)
UPDE vs. Haq sea level (EK)	-0.939 (p<0.001)	-0.854 (p<0.001)
UPDE vs. Haq sea level (LK)	0.015 (p=0.962)	0.036 (p=0.940)
Haq vs. Miller sea level (LK)	0.063 (p=0.854)	0.030 (p=0.941)
Residual DBCs vs. Haq	-0.394 (p=0.003)	-0.227 (p=0.022)
Residual DBCs vs. Haq (J)	0.088 (p=0.698)	0.078 (p=0.638)
Residual DBCs vs. Haq (K)	0.472 (p=0.032)	0.326 (p=0.030)
Residual DBCs vs. Haq (EK)	0.629 (p=0.025)	0.394 (p=0.083)
Residual DBCs vs. Haq (LK)	0.371 (p=0.258)	0.333 (p=0.172)
Residual DBCs vs. Miller (LK)	-0.371 (p=0.228)	-0.212 (p=0.384)
Residual DBFs vs. Haq (K)	0.453 (p=0.026)	0.326 (p=0.025)
Residual DBFs vs. Haq (EK)	0.790 (p=0.006)	0.606 (p=0.010)
Residual DBFs vs. Haq (LK)	-0.259 (p=0.407)	-0.091 (p=0.728)
Residual DBFs vs. Miller (LK)	-0.133 (p=0.665)	-0.152 (p=0.523)

The sea level curve of Haq *et al*. (1987) has been compared with 'corrected' diversity (UPDE, residuals and rarefaction: see Fig. 4.7). There is a negative correlation between sea level and the UPDE for the Mesozoic (Table 4.3). Sea level is positively correlated with the UPDE for the Jurassic, but becomes much more strongly correlated when the Cretaceous and, in particular, the Early Cretaceous are examined. However, there is no

correlation between diversity and sea level when comparisons are limited to the Late Triassic–Early Jurassic or Late Cretaceous time intervals.

There is only a weak negative correlation between DBC-based residuals and sea level for the Mesozoic (Table 4.3). There is no correlation when the two are compared for the Jurassic or Late Cretaceous separately, but there is a statistically significant positive correlation between DBC-based residuals and sea level in the Early Cretaceous (Table 4.3). A moderately strong positive correlation between DBF-based residuals and sea level is recorded for the Cretaceous (Table 4.3). This correlation disappears when the Late Cretaceous is examined by itself, but is greatly reinforced when only the Early Cretaceous is considered (Table 4.3).

As a consequence of the rarefied datasets excluding various stages because of sample sizes, a meaningful statistical comparison with sea level cannot be implemented. However, comparison of the individual peaks and troughs are included in the Discussion.

Discussion

'Corrected' diversity through time

Late Triassic

The UPDE and YPDE both show an initial increase in diversity from the Carnian to a peak in the Norian, before a steep decline in the Rhaetian (Fig. 4.2). This pattern was also noted by Barrett and Upchurch (2005) and Barrett *et al*. (2009). However, consideration of residuals suggests that genus richness was low in the Carnian, while diversity in the Rhaetian appears to be partly controlled by sampling biases. Diversity in the Norian does appear to be genuinely high though (Figs. 4.5 and 4.6) and reflects the diversification of 'prosauropods' and basal sauropodomorphs.

Early Jurassic

The UPDE shows a slight increase in diversity from the Rhaetian (but less than the Norian peak), whereas the YPDE shows a continued decline (Fig. 4.2). The BPDE also shows a Hettangian increase in genus richness. Following this increase, the UPDE curve remains relatively flat, whereas the YPDE continues to decline until a diversity increase in the Pliensbachian (Fig. 4.2). Barrett *et al*. (2009) demonstrated a similar diversity plateau as in the UPDE but differed in showing a notable Toarcian decline. Residuals and rarefaction indicate that diversity in the Hettangian–Sinemurian is controlled by sampling, while the Pliensbachian–Toarcian peak appears genuine (Figs. 4.5 and 4.6), perhaps reflecting the onset of eusauropod diversification.

Middle Jurassic

Although the YPDE and WPDE both show a steep drop in diversity in the Aalenian (by which point non-eusauropod sauropodomorphs have become extinct: Barrett and Upchurch 2005), UPDE shows diversity levels comparable to the Toarcian (Fig. 4.2). Although the extinction of basal forms explains why the YPDE drops at this point, this cannot be used for understanding the differences between the other two curves; this peak in the UPDE can be explained by the inclusion of *Bellusaurus*, which is discussed later. Following this, the UPDE and WPDE both show an increase in diversity, with a peak in the Bathonian–Callovian, reflecting the neosauropod radiation (Fig. 4.2). Rarefaction also demonstrates this same peak, while residuals indicate a diversity peak throughout the Middle Jurassic (Figs. 4.5 and 4.6).

Late Jurassic

The UPDE and WPDE show a severe decline in diversity in the Oxfordian (Upchurch and Barrett 2005; Barrett *et al*. 2009). Both curves then show a recovery in the Kimmeridgian–Tithonian (Fig. 4.2); the UPDE here is equal to the Norian peak. The Oxfordian was recovered as a trough in diversity in both the residuals and rarefaction analyses, suggesting that this is a genuine time of depauperate diversity (Upchurch and Barrett 2005) (though see 'Good rock record versus poor fossil dating' below). Both residuals and rarefaction indicate that the Kimmeridgian–Tithonian diversity peak is a real biological event (Figs. 4.5 and 4.6), and not an artefact of sampling.

Early Cretaceous

Both the UPDE and WPDE show a large drop in diversity at the J/K boundary, with taxon richness remaining low at least until the Barremian (Fig. 4.2). Wagner (2000b) has

argued that PDEs should be conservative in detecting mass extinctions, as a consequence of the backward smearing of origination times which diminish the scale of the mass extinction (note that this can only occur if some lineages survive: if the whole group goes extinct, then there are no lineages left to 'backsmear'). This would suggest that the J/K event potentially represents a genuine extinction (Upchurch and Barrett 2005; Barrett *et al*. 2009). However, the UPDE and WPDE show a relatively high percentage of ghost lineages in the earliest Cretaceous (in particular the Berriasian: five ghost lineages compared to two actual fossil occurrences [UPDE]). The increased 'gappiness' in the fossil record immediately after mass extinctions has been shown to reflect taphonomic bias (Twitchett *et al*. 2000), as Lazarus taxa that temporarily disappear tend to be found in environments that also temporarily disappear (Smith *et al*. 2001). Thus, this Berriasian 'gappiness' may result from lack of preservation of the environments, rather than fluctuations in taxon abundances (Smith 2001). Consideration of the results from the residuals and rarefaction, though, indicates that this diversity 'crash' at the J/K boundary is genuine (Figs. 4.5 and 4.6), as is the resultant depauperate fauna throughout the earliest Cretaceous. The J/K event coincides with the extinction of non-neosauropods, basal macronarians and diplodocids (though see Upchurch and Mannion [2009] regarding the fossil record of the latter clade). Although Raup and Sepkoski (1986) included the J/K boundary as one of their 8 major episodes of marine extinction in the last 250 Myr, most subsequent studies have regarded it as only a minor event (e.g. Hallam & Wignall, 1997; Bambach, 2006; Arens & West, 2008; but see Orcutt, Sahney & Lloyd [2007] for a dissenting view). There is evidence for a large

impact crater at the J/K boundary, around the region of Morokweng, in the Northwest Province of South Africa (Hart et al., 1997; Koeberl, Armstrong & Reimold, 1997; Maier et al., 2006) and it is possible that this impacted on sauropod diversity. As well as the demise of certain sauropod groups, stegosaur diversity was also greatly reduced at the J/K boundary (Bakker, 1978; Galton & Upchurch, 2004b), although why the diversity of other dinosaur clades remained unaffected (Barrett *et al*., 2009; Butler *et al*., 2009b) is difficult to determine (though Orcutt et al. [2007] suggested that large-bodied theropods were also affected); it may relate to differences in the feeding strategies and/or preferred plant fodder of stegosaurs and certain sauropod groups relative to other ornithischian clades and sauropods with narrow tooth crowns that survived into the Cretaceous (see also discussions in Barrett & Willis, 2001; Butler *et al*., 2009b). Large-bodied mammals and marine reptiles were also affected at the J/K boundary (Orcutt *et al*. 2007; Benson *et al*. 2010).

The WPDE shows a small peak in diversity in the Aptian, while diversity in the UPDE remains the same as in the Barremian (Fig. 4.2). Both then show a drop in the Albian. Rarefaction indicates a diversity peak in the Aptian, while Albian diversity cannot be distinguished from Early Cretaceous levels (Fig. 4.6); however, residuals suggest that both of these time periods are at least partly controlled by sampling biases (Fig. 4.5).

Late Cretaceous

Diversity remains low during the Cenomanian–Santonian in both the UPDE and WPDE (Fig. 4.2), while residuals indicate that much of this time interval is influenced by sampling biases (Fig. 4.5). Rarefaction does not enable differentiation of Cenomanian or Santonian diversity from that of the Albian or earliest Cretaceous levels, but Turonian–Coniacian diversity is recovered as comparable with the Aptian (Fig. 4.6). Both PDEs show increases in sauropod diversity in the Campanian. The UPDE exhibits a drop in diversity from the late Campanian to the early Maastrichtian, while diversity remains constant in the WPDE. Both curves show a drop in sauropod diversity in the late Maastrichtian before their demise at the K/P boundary (Fig. 4.2). Residuals indicate low diversity in the early Campanian and late Maastrichtian, with the time interval in-between (i.e. late Campanian–early Maastrichtian) affected to some degree by sampling biases (Fig. 4.5). Rarefaction shows diversity levels indistinguishable from the Aptian and there is no evidence for a decline in diversity across the Campanian–Maastrichtian (Fig. 4.6).

The Maastrichtian drop in diversity observed in the PDEs (Fig. 4.2) may result from an exaggeration of the Signor-Lipps effect (Signor and Lipps 1982; Lane *et al*. 2005). Specifically, in the Maastrichtian (in the lead-up to the K/P mass extinction event), there is a high probability that the taxon will be unsampled. Lane *et al*. (2005) underlined the point that at extinction events many taxa become extinct simultaneously: this results in an increase in 'zombie' lineages and has the effect of making a sudden mass extinction appear prolonged (Signor and Lipps 1982). Lane *et al*. (2005) also highlighted (and demonstrated through computer simulation) that an increased proportion of these 'zombie' lineages belong to terminal taxa at a mass extinction, and it is these that the PDE cannot account for.

Does choice of phylogeny make a difference?

Although most of the phylogenies used in this study result in approximately similar diversity curves, there are a number of times where they differ. In some instances this merely reflects the inclusion of a greater number of taxa, but in several time-intervals these dissimilarities are a result of key differences within the competing phylogenies: these are discussed below.

The UPDE and YPDE curves match each other extremely closely throughout much of the time period under investigation (Table 4.1), although the YPDE tends to estimate a higher number of lineages throughout. This may partly reflect the greater number of taxa (32) incorporated into the Yates (2007) analysis compared to that of Upchurch *et al*. (2007a: 26 taxa), but also the pectinate nature of the former phylogeny, which results in an increased number and duration of ghost lineages. Similarly, following an increase in the Hettangian, the UPDE curve remains relatively flat, while the YPDE continues to decline from the Norian peak until a diversity increase in the Pliensbachian (Fig. 4.2). This difference in timing perhaps relates to the inclusion of different taxa, but probably more strongly reflects a lack of crownward resolution in the Yates (2007) tree.

The UPDE recovered an Aalenian diversity peak, which is not found in the WPDE (Fig. 4.2). This peak is almost entirely caused by the inclusion of the Chinese taxon *Bellusaurus* (see discussion in Upchurch and Barrett 2005) in the former analysis. *Bellusaurus* was recovered from the 'Wucaiwan' Formation of China, which has been dated with no more accuracy than Middle Jurassic (Dong, 1992; Zhao, 1993; Weishampel *et al*., 2004a), meaning its temporal span extends from the Aalenian to the Callovian. Furthermore, Upchurch *et al*. (2004a) recovered it as a basal macronarian, representing a very derived position for a Middle Jurassic sauropod. Dong (1992) stated that the upper contact of the 'Wucaiwan' Formation is overlain by the Shishigou Formation. The base of this latter formation was dated as Bathonian-Callovian by Eberth

et al., (2001). This suggests that an Aalenian date may not be unfeasible, although recent work (Clark *et al*., 2004) has proposed that the 'Wucaiwan' is synonymous with the lower part of the Shishigou Formation, which would indicate a Bathonian-Callovian age for *Bellusaurus*. This combination has the effect of extending all neosauropod lineages back into the Aalenian in the UPDE (Upchurch and Barrett 2005). However, re-analysis of the Upchurch *et al*. (2004a) data matrix has placed *Bellusaurus* outside of Neosauropoda (Wilson and Upchurch 2009), which would reduce the difference between the two diversity curves. Future studies may also wish to use a Bathonian-Callovian age for this taxon, although it should be noted that in the current study this only has a significant impact on UPDE; TDE, residuals and rarefaction are only slightly affected by extending *Bellusaurus* back into the Aalenian as these methods do not rely on phylogenetic relationships.

In most places the LPDE is significantly inflated, even compared to the TDE: this is unexpected given that the latter contains 76 more sauropodomorph taxa than the supertree (Fig. 4.2). The main departure occurs in the late Early Cretaceous: the LPDE shows a prominent diversity peak in the Valanginian–Barremian not seen in the WPDE or UPDE, although minor peaks have been noted for this time period before (Hunt *et al*. 1994; Barrett and Willis 2001). Lloyd *et al*. (2008) suggested that this Valanginian peak may reflect the origination of Lithostrotia, though (aside from the 'Toba sauropod' discussed below) definite lithostrotian remains are yet to be recovered from earlier than the Barremian ('*Titanosaurus valdensis*' from the Isle of Wight, UK: Huene 1929; Wilson and Upchurch 2003). Both the overall diversity inflation and the late Early Cretaceous peak in the LPDE are probably caused by extensive, numerous ghost lineages. For example, the inclusion of the Early Cretaceous 'Toba sauropod' (Tomida and Tsumura 2006) as a derived taxon (i.e. Lithostrotia) in the supertree, pulls nearly all titanosaur lineages back into the Hauterivian. However, this taxon is extremely fragmentary and has not been rigorously placed in a phylogeny. Furthermore, the preserved material shows no evidence to suggest referral to Lithostrotia, and it probably represents either a

basal titanosaur (Tomida and Tsumura 2006) or titanosauriform (Wilson and Upchurch 2009). Other ghost lineages in the LPDE are produced by unusual groupings of taxa, e.g. the Nemegtosauridae being recovered as the sister taxon to *Bellusaurus* + traditional titanosaurs, which pulls some of these clades back into the Aalenian. The production of novel clades, not seen in any of the source trees, is one of the key problems in the construction of supertrees (Bininda-Emonds and Bryant 1998; Pisani and Wilkinson 2002; Pisani *et al*. 2002). The extensive ghost lineages suggest that the late Early Cretaceous diversity peak of the LPDE is probably a partial artefact of an inaccurate phylogeny (Wills 2007). Additionally, the LPDE deviates noticeably from the overall non-avian dinosaur diversity curve of Lloyd *et al*. (2008), suggesting that the study of different taxonomic rankings of dinosaurs will better elucidate fluctuations in dinosaur diversity (see also Barrett *et al*. 2009).

The UPDE suggests a slight recovery in diversity by the Turonian compared to the WPDE (Fig. 4.2); however, this 'recovery' results from the 'diplodocoid' nemegtosaurid ghost lineage extending from the Campanian to the Oxfordian (Upchurch *et al*. 2004a), whereas nemegtosaurids have now been convincingly allied with titanosaurs (Curry Rogers and Forster 2001; Curry Rogers 2005; Wilson 2005).

Does sea level control diversity?

Previous authors (Haubold 1990; Hunt *et al*. 1994; Barrett and Willis 2001; Upchurch and Barrett 2005) have commented on the correlation of a number of peaks and troughs in sauropodomorph diversity with fluctuations in sea level (see 'Materials and Methods'). Of these, only the Kimmeridgian seems to show a correspondence between high diversity and high sea level in the updated analyses (Fig. 4.7), while a late Maastrichtian transgression may correlate with a drop in diversity (though the various methods show conflicting diversity patterns at this time: see above). These correlations suggest that sea level changes could be exerting a genuine biotic effect on diversity: in

the Kimmeridgian, high sea levels might have led to the isolation of terrestrial areas, resulting in allopatric speciation, whereas low sea level in the late Maastrichtian may have enabled the biotic mixing of previously separate regions, leading to extinction (Bakker 1977; Horner 1983; Weishampel and Horner 1987; Upchurch and Barrett 2005). However, several time intervals represent periods of high diversity during low sea level (late Norian and Bathonian–Callovian), while other depauperate times coincide with high sea level (Oxfordian, Berriasian and Cenomanian–Santonian). These negative correlations may also reflect the biotic effect of fluctuating sea levels, i.e. high sea levels can also result in the reduction of habitat size, leading to extinction (Dodson 1990; Upchurch and Barrett 2005) (note that this extinction effect would be expected to only affect diversity at the onset of the transgression, but it is not possible to detect changes at such a fine scale). However, abiotic factors may also play a role, i.e. high sea levels result in a diminished terrestrial record and vice versa (Markwick 1998). The lack of support for other previously reported correlations is possibly a consequence of changes in the geological timescale since that of Haq *et al*. (1987) (see 'Materials and Methods'). Although there is no apparent correspondence between peaks and troughs in the Early Cretaceous, statistical comparisons do suggest that sea level may be controlling diversity fluctuations during this epoch.

The late Turonian and late Coniacian represent the lowest sea levels for the Late Cretaceous (Fig. 4.7). Previous authors (Haubold 1990; Hunt *et al*. 1994; Upchurch and Barrett 2005) have noted that this corresponds with a decline in sauropod diversity; however, the UPDE, residuals and rarefaction (Figs. 4.2, 4.5 and 4.6) show diversity during this time interval to be at least comparable to the Cenomanian and Santonian (both representing times of higher sea levels). These authors (Haubold 1990; Hunt *et al*. 1994; Upchurch and Barrett 2005) also commented on the correlation between high sea levels and high sauropod diversity in the Campanian–Maastrichtian. This time interval does represent a period of higher sea level than most Late Cretaceous stages, which suggests there may still be some correlation. However, the comparably depauperate

Cenomanian records considerably higher sea levels than the Campanian–Maastrichtian (Fig. 4.7), and there is still no statistical correlation between sea level and diversity for the Late Cretaceous when the Cenomanian is excluded. This overall lack of correlation for the Late Cretaceous supports the results presented in Chapter 3 which indicate that titanosaurs (which constituted nearly all Late Cretaceous sauropods) showed a preference for inland terrestrial environments, and thus sea level would be expected to have a limited or indirect effect on their diversity.

It should be noted, though, that there is no correlation between the Late Cretaceous sea level curves of Miller *et al*. (2005) and Haq *et al*. (1987) (see Table 4.3). This discrepancy suggests that future studies may produce different sea level curves for the rest of the Mesozoic too, which could challenge some of the above results.

Good rock record versus poor fossil dating

An additional issue, which must at least partly have an impact on the diversity curves, relates to problems with the dating of many fossil-bearing localities (see also 'Materials and Methods'). Several stages (e.g. the Oxfordian) with good rock records (i.e. time periods with a significant amount of sedimentary rock representing suitable depositional environments for the preservation of dinosaurs) have low apparent (and 'corrected') diversity, indicating that these are genuinely depauperate time periods. However, it is possible that at least some of these time intervals reflect the effects of poor dating instead. For example, as noted above (and in previous studies), sauropod diversity is extremely low in the Oxfordian, yet it is possible that many Late Jurassic outcrops dated as Kimmeridgian–Tithonian actually include Oxfordian sediments too. The Late Jurassic Morrison Formation of North America provides a suitable case study: this formation has produced 11 of the 175 genera included in this study and is generally considered Kimmeridgian–Tithonian in age (see reviews in Kowallis *et al*. 1998; Weishampel *et al*. 2004a, b). However, a recent study using U/Pb SHRIMP analyses of 8

individual zircon crystals collected from the upper third of the formation (exposed at Ninemile Hill, near Medicine Bow, southeastern Wyoming) yielded a date of 156.3 +/- 2 Ma, which indicates that at least some of the Morrison Formation is probably Oxfordian (Trujillo *et al*. 2006). Earlier studies have also hinted at the possibility of an Oxfordian age for the lower parts of the formation (Imlay 1980; Hotton 1986; Kowallis *et al*. 1998; Litwin *et al*. 1998; Schudack *et al*. 1998). Similar problems affect the Middle Jurassic of China, where many formations are dated no more accurately than at the epoch level. The Middle Jurassic appears to represent the onset of the neosauropod radiation (Wilson & Sereno 1998; Day *et al*. 2002) and so poor dating of this time period may obscure the timing of evolutionary events. However, this may not be so problematic in China where all Jurassic sauropods appear to lie outside Neosauropoda (though see earlier discussion of *Bellusaurus*). There may be comparable problems in outcrops in other countries, as well as other time periods (e.g. the Early Cretaceous of North America, as well as the Cretaceous of China and South America). This is an effect that cannot be accounted for by the current analyses and raises issues regarding how genuine some of the diversity patterns are.

Methodological choices

Different approaches to correcting diversity

The three methods utilised here for 'correcting' diversity (PDE, residuals and rarefaction) all capture different aspects of sampling biases and thus each has its benefits. Phylogeny may be detached from sampling in the strictest sense, but its inference of ghost lineages fills gaps in our sampling of the fossil record and is particularly useful for elucidating diversity in time periods with a poor rock record. Residuals allow the 'removal' of sampling biases from observed diversity, enabling the investigation of how diversity might appear given an unbiased record, while problems pertaining to varying sample size can be resolved through rarefaction. Each method has

its problems (see 'Materials and Methods') but use of all three techniques allows us to benefit from each of their strengths and enables recognition of peaks and troughs common to all.

In the case of rarefaction, the 'all-occurrences' analysis seems a more meaningful way of implementing rarefaction than the 'generic-only' analysis in that it does not exclude data. Future studies may wish to refine this method by considering generically indeterminate representatives of each clade as a different taxon, e.g. the presence of three indeterminate diplodocids, two indeterminate dicraeosaurids and one indeterminate titanosaur at a locality would increase diversity by three.

Time-slicing

Although previous studies have described and compared individual peaks and troughs in diversity and sampling proxies (e.g. Upchurch and Barrett 2005; Barrett *et al*. 2009; Butler *et al*. 2009c), statistical comparisons have usually been restricted to the full time interval under investigation (e.g. the Late Triassic–Late Cretaceous in the case of Barrett *et al*. 2009). It is possible that such a comparison will produce non-significant results because the particular sampling bias does not affect diversity throughout the full time period under investigation. However, if this bias exerted an influence for just the Cretaceous, for example, then any signal might be obscured by the remaining time interval. This problem can be ameliorated by time-slicing the statistical correlations (see also Chapter 3), as has been implemented in the current study. There are a number of examples where a full Mesozoic comparison has resulted in no relationship, while consideration of a smaller time bin has demonstrated a strong correlation (e.g. TDE vs. DBFs for the Cretaceous: Table 4.2). This approach could have implications for recent studies (e.g. Marx 2009), which have reported no statistical correlation between diversity and sampling biases.

CHAPTER FIVE

COMPLETENESS METRICS

Parts of this chapter form the basis for the following paper:

Mannion, P. D. and Upchurch, P. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology* 36, 283-302.

(1) The quality of the sauropodomorph fossil record through geological time

Analyses and Results

Average SCM1, SCM2, CCM1 and CCM2 scores have been calculated for each substage and then plotted against time (Fig. 5.1). Table 5.1 gives a full list of the statistical comparisons made between the curves of the different completeness metrics through geological time. These have been statistically compared with the sauropodomorph taxic diversity curve (see 'Materials and Methods'), as well as the sea level curve of Haq *et al*. (1987), the western European rock outcrop area dataset of Smith and McGowan (2007) and numbers of dinosaur-bearing collections (DBCs; see 'Chapter Four'). As well as examining completeness scores for sauropodomorphs as a whole, comparisons have also been made between different groups (e.g. Diplodocoidea versus Macronaria: Table 5.2).

One potential problem with the method of time binning is the variation in duration of stages. For example, the Aptian is 13 Myr while the Bathonian is only 3 Myr in duration. It might be expected that longer stages have a better chance of including more complete specimens and thus perhaps will have higher average scores of completeness. However, there is no correlation between substage duration and completeness (Spearman's $r_s < 0.20$; $p > 0.14$), suggesting that the choice of time bins is not creating artefactual peaks and troughs in longer and shorter substages respectively.

For the most part, all four metrics (SCM1-2 and CCM1-2) closely mirror one another through time (Fig. 5.1; $p < 1x10^{-4}$ for all tests: Table 5.1) and runs tests demonstrate a statistically significant deviation from randomness ($p < 2x10^{-6}$).

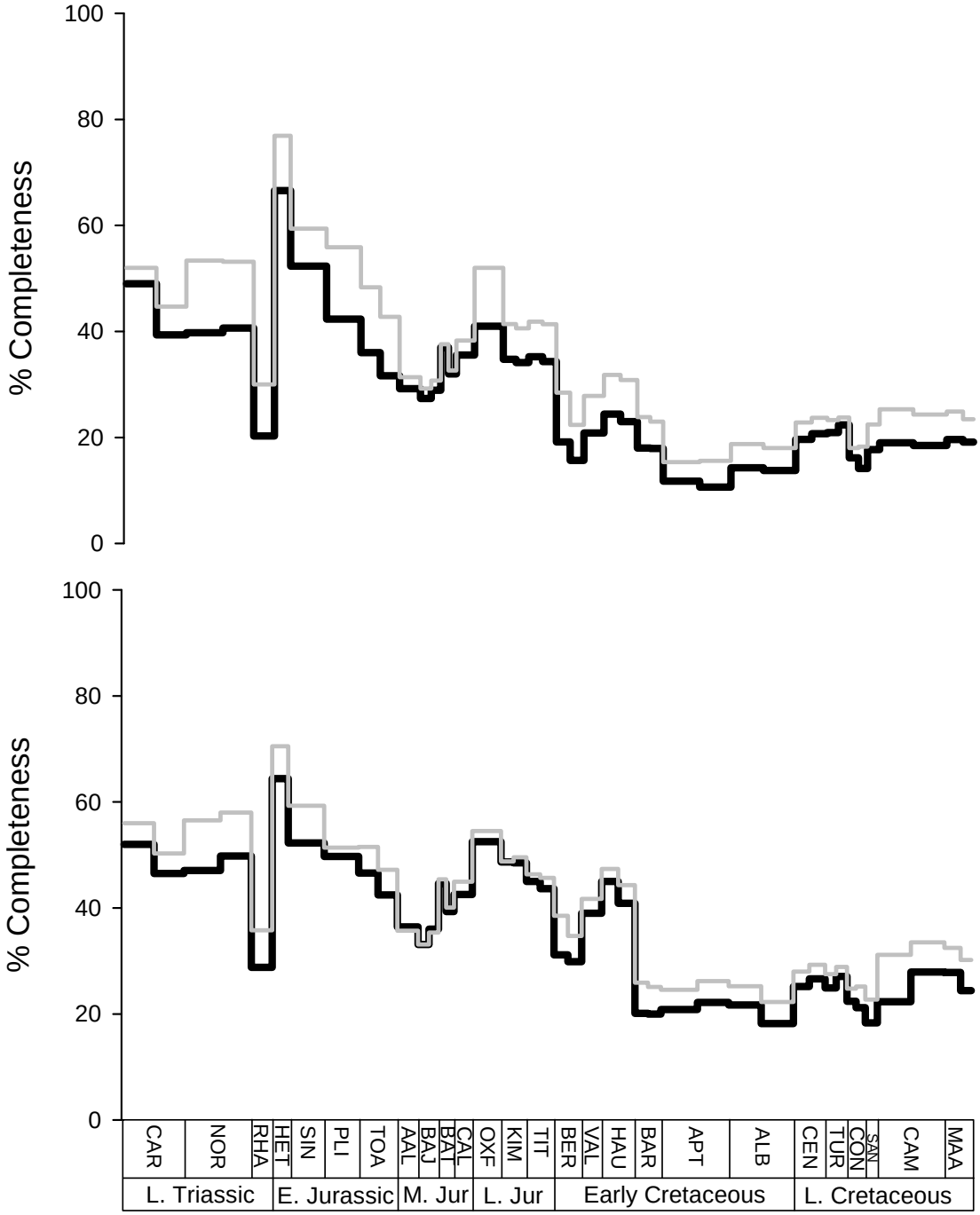

FIGURE 5.1. Completeness of taxa through geological time, using both SCM (black lines) and CCM (grey lines): (A) Most complete individual (SCM1 and CCM1), (B) Percentage of taxon known (SCM2 and CCM2).

Comparison	Spearman's	Kendall's	Pearson's
SCM1 vs. SCM2	0.93970	0.79666	0.91247
SCM1 vs. CCM1	0.96391	0.85595	0.97366
SCM1 vs. CCM2	0.92016	0.75456	0.90778
SCM2 vs. CCM1	0.94299	0.80015	0.92115
SCM2 vs. CCM2	0.97559	0.88264	0.97743
CCM1 vs. CCM2	0.95988	0.83403	0.94859

TABLE 5.1. Results of statistical analyses (Spearman's rank correlation coefficient, Kendall's tau rank correlation coefficient, Pearson's product-moment correlation coefficient) comparing geological completeness curves (SCM1-2 and CCM1-2) with one another. *P*-values are < $1x10^{-4}$ for all tests.

Sauropodomorph diversity

Statistical comparison shows no correlation between diversity and completeness metrics for the Mesozoic ($p > 0.48$ for all tests). When the Mesozoic is divided into smaller time periods no statistically significant correlations are recovered for the Late Triassic, Jurassic or Cretaceous, but there are strong negative and positive correlations when the Early ($p < 0.01$ for all tests) and Late ($p < 0.006$ for all tests, except for SCM1 which produces a non-significant result) Cretaceous, respectively, are examined separately.

Controls on fossil record quality

There is no correlation between any of the completeness metrics (SCM1-2 and CCM1-2) and the rock outcrop area dataset of Smith and McGowan (2007): this is the case for both the terrestrial and marine element of their dataset. There is a strong negative correlation (SC1: Spearman's $r_s > -0.7001$; Kendall's tau > -0.5002; $p < 0.001$) between all

four completeness metrics and the Mesozoic sea level curve of Haq *et al*. (1987). However, when the Mesozoic is divided into smaller time intervals, there are exceptions to this overall pattern. For instance, when the Late Triassic, Cretaceous or Late Cretaceous are analysed individually, there is no correlation between completeness and sea level, whereas the Jurassic and Early Cretaceous retain the negative correlation.

There is also a fairly strong negative correlation between all four completeness metrics and numbers of DBCs for the Mesozoic (SC1: Spearman's r_s = -0.552; Kendall's tau = -0.337; $p < 0.001$). When the Mesozoic is spilt into smaller time intervals a number of finer scale patterns emerge. In the Late Triassic, there is an extremely strong positive correlation, but only for PCM1 and PCM2 (Spearman's r_s = 0.970; Kendall's tau = 0.926; $p < 0.022$). There is a moderately strong positive correlation for all four metrics in the Jurassic (SC1: Spearman's r_s = 0.455; Kendall's tau > 0.333; $p < 0.038$). There is no correlation in the Cretaceous, but there is a strong negative correlation when the Early Cretaceous is analysed separately (SC1: Spearman's r_s > -0.792; Kendall's tau > -0.595; $p < 0.008$).

Interpretation and Discussion

Completeness levels are high in the early Carnian and remain relatively high during the late Carnian-Norian. There is then a prominent decrease in the Rhaetian. This is followed by the highest peak in sauropodomorph completeness in the Hettangian-Sinemurian. The presence of a Hettangian peak in completeness is surprising given that the Early Jurassic is generally perceived as a time of poor fossil record quality, especially for sauropods (Bakker 1977; Upchurch and Barrett 2005), as a consequence of the relatively limited geographic sampling of terrestrial sediments of this age (see Weishampel *et al*. 2004a). However, the high score can partly be attributed to the presence of many well-preserved prosauropod and basal sauropod skeletons from the upper Elliot and Clarens formations of South Africa (e.g. *Massospondylus*) and Lower Lufeng Formation of the People's Republic of China (e.g. *Lufengosaurus* and *Jingshanosaurus*) (Galton and Upchurch 2004; Upchurch *et al*. 2007a; Yates 2007). There is a steady decrease in completeness levels throughout the remainder of the Early-Middle Jurassic until a rise in the Bathonian (Fig. 5.1A, B), which culminates in an Oxfordian peak. The early Middle Jurassic low point matches a particularly poor part of the sauropod fossil record according to Upchurch and Barrett (2005), who noted that ghost ranges are relatively high compared to observed lineages for this time interval (see Chapters 1 and 4). High completeness levels in the Oxfordian might seem anomalous given the presence of only two sauropod taxa for this stage (*Mamenchisaurus* and *Daanosaurus*). However, Upchurch and Barrett (2005) noted that the 'number of opportunities to observe' (based on using DBFs as a proxy) was higher for this time period than for any other Jurassic stage, and suggested that the Oxfordian (despite a good rock record) may represent a genuine trough in sauropod diversity (see also Chapter 4). Completeness remains high for the Late Jurassic before a large decrease at the Jurassic/Cretaceous (J/K) boundary: this is a particularly prominent drop for SCM1 and CCM1 (Fig. 5.1A) but is less marked for the other two metrics (Fig. 5.1B). Sauropods apparently underwent a dramatic decrease in observed taxic diversity (80%) and

phylogenetic lineage diversity (60%) at the J/K boundary (Upchurch and Barrett 2005; Barrett et al. 2009; see also Chapter 4). Comparisons based on the number of Late Jurassic and Early Cretaceous DBFs suggest that this observed diversity decrease represents a genuine extinction (Upchurch and Barrett 2005). It could be argued that the apparent decrease in sauropod fossil record quality across the J/K boundary, based on the completeness metric scores, represents a contradictory signal that suggests that the diversity decrease is a sampling artefact. However, the use of completeness metrics as sampling proxies is a more complex issue than previously recognised: this will be discussed in more detail later.

After the J/K boundary, there is an increase in completeness during the Valanginian-Hauterivian (with a prominent peak for SCM2 and CCM2, though this is much less notable for the other two metrics; Fig. 5.1), before a decline in the Barremian: this is extremely severe in the case of SCM2 and CCM2, with completeness halving in the former metric (Fig. 5.1B). SCM1 and CCM1 show a further decline in completeness into the Aptian. This is interesting because Upchurch and Barrett (2005) noted that taxic diversity for sauropods shows a peak during the Aptian-Albian, but phylogenetic diversity estimates display a gradual decline from the Hauterivian to the Cenomanian, paralleling the completeness scores (see also Chapter 4). After a small increase in the Cenomanian, completeness scores decrease again from the Turonian to Santonian. Indeed, early Late Cretaceous levels of completeness are consistently lower than at any other point during sauropodomorph evolution. This is not surprising given that, until relatively recently, there were no diagnosable sauropod genera known from the Turonian and Coniacian because the few specimens that had been found were extremely fragmentary (e.g. Huene 1929). This situation has changed through the discovery of new and better preserved material, the re-dating of some formations in South America, and taxonomic revision (e.g. Leanza and Hugo 2001; Apesteguía 2007; Calvo *et al*. 2007), but it is interesting to note that these developments have not yet raised the quality of the early Late Cretaceous fossil record to levels comparable with

the Jurassic or latest Cretaceous (probably because there have also been important discoveries from other time periods which have raised the quality of the fossil record relative to that for the early Late Cretaceous). Although there are minor differences between the various completeness metric scores, there is a moderate increase in fossil record quality for the Campanian and Maastrichtian. This matches a peak in sauropod taxic diversity at this time (see Chapter 4), reflecting recent discoveries of many new titanosaurian genera from Madagascar, India, China and South America (e.g. Curry Rogers and Forster 2001; Wilson and Upchurch 2003; Xu *et al*. 2006; Salgado and Carvalho 2008). Most of these taxa, however, are based on partial skeletons and often lack cranial material: thus the completeness scores remain lower than those observed from the Early and Late Jurassic where many, virtually complete, taxa have been recovered. The generally lower levels of completeness in the Cretaceous are slightly unexpected, given that the number of DBFs was shown to be higher for this period than for the rest of the Mesozoic (Upchurch and Barrett 2005) (but see below for further comments on the relative completeness scores for the Jurassic and Cretaceous). On the other hand, this trend of an Early Jurassic peak in completeness, followed by a decline into the Early Cretaceous, shows similarities to the pattern of increasing 'gappiness' found by Wills (2007) for a large range of taxa, which suggests that the Cretaceous sauropod fossil record is poorer than that of the Jurassic.

Completeness within different sauropodomorph groups

Table 5.2 lists completeness scores for the six metrics for a number of different sauropodomorph groups. Sauropodomorphs lying outside of Sauropoda are, on average, considerably more complete than more derived forms (see also Chapter 8), while non-neosauropod sauropodomorphs also tend to be known from much more complete specimens than neosauropods. Within Neosauropoda, diplodocoids are known, on average, from slightly more complete material than macronarians; however, both tend to be based on similarly complete type material. The average completeness of

titanosaurs (derived macronarians) is slightly lower than for Macronaria as a whole, and non-titanosaurs are generally known from considerably more complete material than titanosaurs (see also Chapter 8). This is interesting because the majority of titanosaurian taxa are Cretaceous in age, whereas most non-titanosaurs are from the Late Triassic and Jurassic. The Cretaceous fossil record of sauropodomorphs might have been expected to be higher in quality than that for the Triassic and Jurassic because Cretaceous sediments have had less time to be destroyed by geological processes (the 'Pull of the Recent' [Raup 1972]; though see Benton *et al*. [2000] for a contradictory signal regarding the quality of the fossil record through time). However, as noted above, it seems that the Cretaceous fossil record of sauropodomorphs is poorer than that from earlier periods, and this inevitably has a disproportionate effect on the completeness scores for titanosaurs. This may explain why, despite intense taxonomic and phylogenetic work over the past two decades (e.g. Calvo and Salgado 1995; Upchurch 1995, 1998; Salgado *et al*. 1997; Wilson and Sereno 1998; Curry Rogers and Forster 2001; Wilson 2002; Upchurch *et al*. 2004a; Curry Rogers 2005; Calvo *et al*. 2007) titanosaurs remain a relatively poorly understood group in comparison to most other regions of the sauropodomorph evolutionary tree (Upchurch *et al*. 2004a; Curry Rogers 2005). One possibility is that this reflects a Northern-Southern Hemisphere asymmetrical bias: sauropods are often perceived as being a predominantly Gondwanan radiation by the time of the Cretaceous (e.g. Bonaparte and Kielan-Jaworowska 1987) and the Southern Hemisphere fossil record is less well sampled than that of the Northern Hemisphere. However, an examination of the distribution of Cretaceous sauropods reveals that 45 genera are known from Gondwana compared to 39 from Laurasia; thus, there is little difference between the two palaeocontinents and geographic distribution does not appear to have a notable impact on Cretaceous diversity. Chapter 3 presented evidence that titanosaurs displayed a preference for inland environments, in comparison to non-titanosaurs. This ecological difference may have decreased the probability of titanosaurian material being successfully fossilised, which may explain the lower

completeness score for titanosaurs and thus the relative poverty of the Cretaceous sauropodomorph fossil record, despite comparatively high numbers of DBFs.

Group	SCM1	SCM2	SCM_{ts}	CCM1	CCM2	CCM_{ts}
Non-Sauropoda	47.17	54.36	34.71	57.57	61.16	43.43
Non-Neosauropoda	35.25	43.00	27.11	42.25	47.30	33.13
Neosauropoda	20.40	28.90	15.14	25.49	32.32	19.47
Diplodocoidea	25.25	35.90	15.95	30.65	37.19	19.20
Macronaria	18.92	27.13	14.73	23.80	30.98	19.23
Non-Titanosauria	30.69	39.03	22.66	36.91	42.73	27.56
Titanosauria	17.52	24.42	14.12	22.62	29.09	19.31

TABLE 5.2. Average completeness percentages for a selection of sauropodomorph clades and grades.

Controls on fossil record quality

The above results suggest that sea level has, in some fashion, controlled the quality of the sauropodomorph fossil record, but only through part of the group's evolutionary history, with high sea level correlated with low average completeness scores, and low sea level with high completeness scores in the Jurassic-Early Cretaceous. Hunt *et al*. (1994) proposed that sauropod diversity correlated positively with sea level because more material could be preserved during times of higher sea level; however, these results directly contradict this suggestion.

One possibility is that periods of high sea level produced conditions that promoted low diversity and abundance among sauropodomorphs; however, it is difficult to find convincing biological mechanisms to underpin this hypothesis. Upchurch and Barrett (2005) noted that higher sea levels promote the fragmentation of land areas via the

formation of geographic barriers. As well as producing allopatric speciation, this may conversely also result in extinction events as the sizes of some habitats dwindle. A more probable, abiotic, explanation is that sea level affects the preservation potential of terrestrial organisms. For example, Markwick (1998) has suggested that the fossil record of terrestrial taxa will be poorer during times of high sea level, as a consequence of the greatly diminished availability of land area on which to preserve a terrestrial record.

The lack of correlation between completeness and sea level in the Late Cretaceous is consistent with the dominance of titanosaurs during this time and the apparent preference of this group for inland habitats (see Chapter 3). It is also comparable with the lack of correlation between diversity and sea level for this time interval (see Chapter 4). It is likely that the preservation potential of a terrestrial group that occupies habitats away from coastal lagoons, deltas, etc. will be less strongly affected by fluctuating sea levels.

The positive correlation between completeness and numbers of DBCs in the Late Triassic-Jurassic suggests that we have a better chance of finding complete specimens of taxa with increasing numbers of opportunities to observe, as would be expected. However, the negative correlation in the Early Cretaceous is somewhat surprising and is perhaps indicative of other factors (e.g. sea level) exerting an influence that over-rides collecting effort.

A lack of correlation between completeness and outcrop area may mean that the two are unrelated; however, the latter data are based solely on the western European rock record and as such may not be representative of the global record. Thus, it is possible that rock outcrop area does have an effect on completeness, but that the outcrop dataset is currently inadequate for testing this hypothesis (see also Chapter 4).

(2) Historical trends in specimen collection and taxonomy

There are at least two factors that lead to the prediction that SCM1, SCM2, CCM1 and CCM2 scores will tend to increase through historical time:

- For each genus the completeness score can only be increased by new discoveries, never decreased. Therefore, as sauropodomorph material accumulates through historical time as a result of collecting effort, there should be a kind of 'ratchet effect' that means that taxa either remain at a given level of completeness or improve, but never decrease in completeness (except in rare cases where material is destroyed or new discoveries that demonstrate a previously named taxon known from multiple localities actually represents a chimera).
- An awareness of the current state of the sauropodomorph fossil record could influence decisions made when collecting new material. Thus, during the early years of the study of sauropodomorphs (i.e. from 1830 to 1870) virtually every specimen might have seemed worthy of collection, irrespective of its level of completeness, partly because most localities would be 'new' in terms of their age or geographic position. In contrast, field crews working today (particularly in well-sampled regions) might deem isolated teeth and vertebrae as relatively unimportant, and instead focus their efforts on finding and collecting skulls and partial or complete skeletons.

Analyses and Results

Specimen quality through historical time

In order to examine the above prediction, SCM1, SCM2, CCM1 and CCM2 have been calculated for sauropodomorph taxa for each of the ten-year time bins from 1830 to the

present (Fig. 5.2A-B), with the statistical support for an increase in average taxon completeness through time assessed. SCM1, SCM2, CCM1 and CCM2 closely follow one another for each historical time bin (Fig. 5.2; $p < 0.001$; Table 5.3), with CCMs tending to produce slightly higher percentages for most decades. Contrary to the prediction that specimen quality should improve through historical time, the results suggest that there is no such trend (Fig. 5.2A-B; Pearson's $r < 0.15$; $p > 0.5$). Additionally, runs tests demonstrate that there is no statistically significant departure from randomness ($p > 0.127$). All four metrics show peaks in the 1830s, 1900s and 1960s, with the 2000s actually being one of the decades with the lowest average completeness scores in each case (Fig. 5.2A, B).

Type specimens through historical time

Benton (2008a) argued that the quality of dinosaurian type material has improved through historical time. This claim is tested for sauropodomorphs by plotting SCM_{ts} and CCM_{ts} against historical time, using the same ten-year time bins employed by Benton (2008a) (Fig. 5.2C). SCM_{ts} and CCM_{ts} display low or no correlation with the other four metrics (Spearman's $r_s = 0.325\text{-}0.449$; $p = 0.064\text{-}0.205$; Table 5.3) but do show a trend of improving completeness through historical time (Fig. 5.2C; Pearson's $r < 0.542$; $p < 0.039$ [N.B. the 1860s have been excluded because no sauropodomorph taxa were named during this decade]), although runs tests indicate that there is no statistical support for any deviation from randomness ($p > 0.9$). SCM_{ts} and CCM_{ts} both show a statistically significant correlation with the trend found by Benton (2008a; $p < 0.022$ for all tests). These results are in broad agreement with Benton's (2008a, b) conclusions regarding dinosaurian type specimens as a whole, although the statistical support for this pattern is considerably weaker in the current analysis and is removed when the Bonferroni correction is applied.

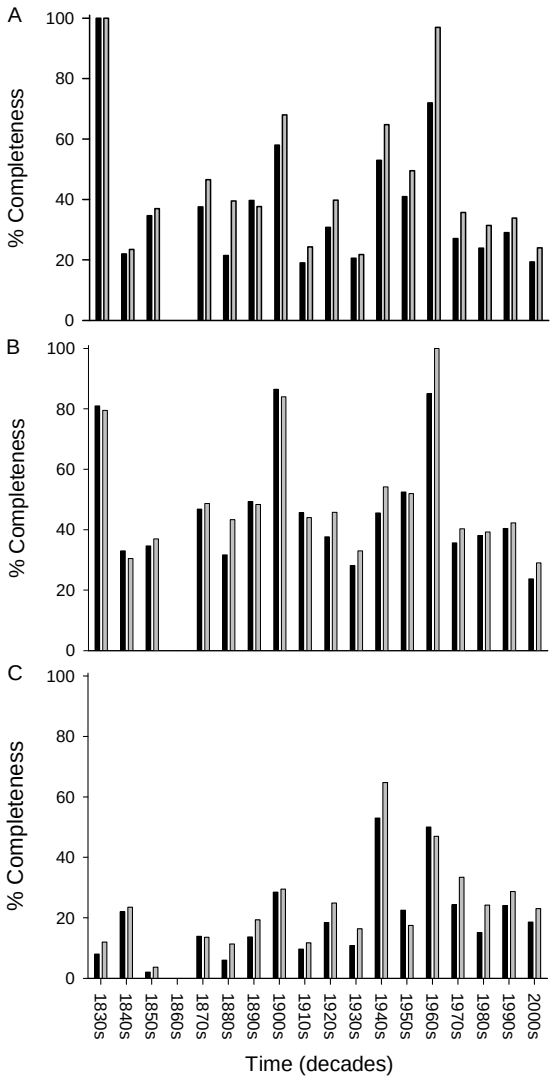

FIGURE 5.2. Completeness of taxa through historical time, using both SCM (black charts) and CCM (grey charts): (A) Most complete individual for SCM1 (Pearson's r = 0.0141; best-fitting line: y = -0.717x + 42.876; *p* = 0.5207) and CCM1 (Pearson's r = 0.0759; best-fitting line: y = -0.2881x + 45.763; *p* = 0.816), (B) Percentage of taxon known for SCM2 (Pearson's r = 0.1028; best-fitting line: y = -0.1418x + 45.547; *p* = 0.8903) and CCM2 (Pearson's r = 0.1459; best-fitting line: y = 0.1983x + 45.407; *p* = 0.853), (C) Completeness of type material for SCM_{ts} (Pearson's r = 0.4956; best-fitting line: y = 1.2823x + 6.7382; *p* = 0.0419) and CCM_{ts} (Pearson's r = 0.4850; best-fitting line: y = 1.4923x + 8.2967; *p* = 0.0193). Note that no valid taxa were named during the 1860s.

A statistically robust trend can be established based on an entire dataset, but this may obscure variation in support for this trend within different parts of the data (for an example, see the earlier comparisons between completeness and sea level through geological time). The SCM_{ts} and CCM_{ts} curves (Fig. 5.2C) demonstrate that there is considerable fluctuation in completeness from 1830 until around 1930, though there is a slight increase from 1850 to 1900. There also appears to be a decline in completeness from the 1940s to the present day. To test these observations, the data were partitioned into two portions, one covering 1830 to 1940 and the other from 1940 to the present, and then each data subset was searched for statistical trends. Neither time interval showed any statistically significant trends in type specimen completeness (Fig. 5.2C; $p > 0.373$ for all Pearson's tests). Similarly, statistically insignificant results were recovered when the dataset was partitioned into 1830-1900 and 1900 to the present ($p > 0.497$ for all Pearson's tests and for both time intervals). The differences between these results for sauropodomorphs and Benton's results for dinosaurs as a whole are most marked for relatively recent historical time. The average completeness of sauropodomorph types in the current decade (2000s) is no different to that of the 1920s and is less than that of the 1840s (Fig. 5.2C), while the 1940s and 1960s represent decades with the highest average completeness (though only one taxon, *Riojasaurus*, was described in the 1960s). In contrast, Benton (2008a) found that the current decade has the second highest ratio of complete to incomplete dinosaurian type specimens. Benton (2008b) also highlighted an improvement in the naming of valid taxa in the last 15 years. To test whether there has been a recent improvement in sauropodomorph type specimen completeness, average completeness for each year from 1970 to 2008 and from 1990 to 2008 was calculated. Neither of these analyses produced any statistical support for a trend towards increasing completeness during these time periods ($p > 0.66$ for all Pearson's tests; $p > 0.27$ for all runs tests). When Benton's data for dinosaurs as a whole is partitioned into subsets covering 1830-1900 and 1900-2004, neither period displayed any statistical trends ($p > 0.10$ for all Pearson's tests). Similarly,

no trends were observed for the time interval extending from 1940 to 2004 (p = 0.31 for Pearson's test).

Comparison	Spearman's	Kendall's	Pearson's
SCM1 vs. SCM2	0.82869 (p<0.001)	0.69935 (p<0.001)	0.96918 (p<1x10^{-4})
SCM1 vs. SCM$_{ts}$	0.44892 (p=0.064)	0.33333 (p=0.061)	0.70192 (p=0.0095)
SCM1 vs. CCM1	0.91538 (p<0.001)	0.80392 (p<0.001)	0.98902 (p<1x10^{-4})
SCM1 vs. CCM2	0.85759 (p<0.001)	0.72549 (p<0.001)	0.96804 (p<1x10^{-4})
SCM1 vs. CCM$_{ts}$	0.42002 (p=0.079)	0.32026 (p=0.066)	0.74117 (p=0.0129)
SCM2 vs. SCM$_{ts}$	0.41796 (p=0.105)	0.26797 (p=0.155)	0.73224 (p=0.0046)
SCM2 vs. CCM1	0.80186 (p<0.001)	0.60784 (p<0.001)	0.97229 (p<1x10^{-4})
SCM2 vs. CCM2	0.91744 (p<0.001)	0.79085 (p<0.001)	0.99418 (p<1x10^{-4})
SCM2 vs. CCM$_{ts}$	0.34985 (p=0.131)	0.25490 (p=0.144)	0.77117 (p=0.0126)
SCM$_{ts}$ vs. CCM1	0.37049 (p=0.135)	0.29412 (p=0.094)	0.71992 (p=0.0070)
SCM$_{ts}$ vs. CCM2	0.43034 (p=0.080)	0.32026 (p=0.068)	0.74173 (p=0.0035)
SCM$_{ts}$ vs. CCM$_{ts}$	0.94014 (p<0.001)	0.83007 (p<0.001)	0.97567 (p<1x10^{-4})
CCM1 vs. CCM2	0.93189 (p<0.001)	0.79085 (p<0.001)	0.98160 (p<1x10^{-4})
CCM1 vs. CCM$_{ts}$	0.32508 (p=0.205)	0.25490 (p=0.157)	0.76518 (p=0.0087)
CCM2 vs. CCM$_{ts}$	0.37688 (p=0.128)	0.28105 (p=0.109)	0.79082 (p=0.0076)

TABLE 5.3. Results of statistical analyses (Spearman's rank correlation coefficient, Kendall's tau rank correlation coefficient, Pearson's product-moment correlation coefficient) comparing historical completeness curves with one another.

Differences between previous work and this study

This study, and those by Benton (2008a, b), may have produced different results because they have employed different methods for assessing type specimen quality. The main methodological differences between this study and those of Benton (2008a, b) are

that average completeness was calculated here, whereas Benton (2008a) uses a ratio of 'good: poor' specimens, and here a relatively fine-grained and less arbitrary percentage-scheme was used to express specimen completeness whereas Benton (2008b) uses a scale from 1 to 5. In addition, Benton (2008a) includes all species, regardless of their validity. The impact of these choices has been evaluated by re-running Benton's analyses based on averages of his 1-5 scale, re-running the current analyses using a ratio of good to: poor specimens (where 'good' and 'poor' are identified as specimens with SCM_{ts} and CCM_{ts} scores for the skull and/or skeleton that are higher or lower than 50% respectively: see Benton 2008a), and re-running the current analyses with invalid species incorporated into the dataset.

Benton's data were used to calculate averaged completeness scores for type specimens (again in 10-year time bins) based on his quality scale from 1 to 5. These data showed strong support for a trend of increased completeness with time (Pearson's $r < 0.844$; $p < 1x10^{-4}$; $p = 6.7x10^{-3}$ for runs test). However, when this modified dataset was partitioned into 1830-1900 and 1900-2004, a trend of improving completeness for the first period ($p = 0.008$) was found, but again no statistical support for any trend for 1900-2004 ($p = 0.6$; $p = 0.35$ for runs test). In addition, no trend was found when average completeness was examined during the time period of 1940-2004 ($p = 0.147$).

SCM_{ts} and CCM_{ts} scores were then used to assign sauropodomorph type specimens to 'good' and 'poor' categories (see above) and ratios were calculated for each decade, in an attempt to replicate the methodology of Benton (2008a). For the period 1830-present, this analysis yielded weak support (Pearson's $r < 0.455$; $p = 0.066$; although runs tests showed no statistical support: $p = 0.9$) for a trend of increasing type specimen completeness. This weak improving trend, however, disappeared completely when the data were partitioned into 1830-1900 and 1900 to the present ($p > 0.41$ for all Pearson's tests).

Finally, SCM_{ts} and CCM_{ts} scores were calculated for all sauropodomorph species from 1940-2008, regardless of whether they are valid or invalid taxa. This modified version of the dataset yielded a trend toward decreasing type specimen completeness in terms of average scores per decade (SCM_{ts}: Pearson's r = -0.825; p = 0.027; CCM_{ts}: Pearson's r = -0.730; p = 0.082), though this trend disappeared when the 1940s were excluded. No statistically robust trends are observed when average completeness scores were analysed per year between 1940 and 2008 (p > 0.58 for all Pearson's tests; p > 0.42 for runs tests), between 1970 and 2008 (p > 0.4 for all Pearson's tests; p > 0.41 for runs tests) and 1990 and 2008 (p > 0.84 for all Pearson's tests; p > 0.66 for runs tests).

Discussion

The results of the analyses investigating SCM1-2 and PCM1-2 suggest that palaeontologists are continuing to collect sauropodomorph material irrespective of its level of completeness. This could be for several reasons, including:

- It is frequently difficult to determine the full taxonomic significance of a specimen while it is in the field, and therefore it is often worth collecting a fragmentary specimen 'just in case'. Furthermore, there is a growing appreciation that the completeness of a specimen is not entirely correlated with its systematic informativeness: for example, even a very fragmentary specimen can play a crucial role in phylogenetic analysis if it possesses an unusual combination of character states (Smith 1994; Upchurch *et al*. 2007b; Carrano and Sampson 2008). Additionally, as our knowledge of sauropodomorphs improves, it might require less of the animal to be preserved to determine whether or not it represents a new taxon.
- There is still a demand from museums for sauropod specimens, even if they are very incomplete.
- There is now a greater appreciation of the importance of consistent and complete sampling if we wish to study relative abundances and other palaeoecological parameters or aspects of taphonomy (e.g. Behrensmeyer *et al*. 2000; Moore *et al*. 2007).
- Much of the recent influx of new data on dinosaurs has occurred through the exploration of new geographic locations (Benton 2008a, b). It seems probable that palaeontologists working in previously unsampled portions of the fossil record will tend to collect a wide range of specimens, irrespective of their completeness, because every new specimen is potentially a new data point.

The four factors listed above may explain why very incomplete specimens are not left in the field as often as one might expect, but they do not counteract the 'ratchet effect' on average completeness scores through historical time. However, average completeness scores will be lowered for a given time bin if systematists name a large number of new sauropodomorph taxa on the basis of relatively incomplete material. Thus, the observation that average SCM and CCM scores fluctuate through historical time, rather than showing a gradual upwards trend, suggests that there are occasional influxes of relatively incomplete new taxa, and the low average score for the current decade implies that one such influx might be occurring at present.

The results from these new analyses and the re-analyses of Benton's data suggest that there is a historical trend towards increasing type specimen completeness, but only when the period of time considered includes the earliest phase of dinosaur discovery and naming (1830 to approximately 1900). However, there is no evidence for such a trend when more recent time periods are examined, including 1900, 1940, 1970 or 1990, to the present. Additionally, decisions regarding ratios versus averages, or fine-grained percentage scales versus coarse-grained category scales, have a minor impact on the results of analyses, but the broad conclusions remain unchanged. Similarly, the inclusion/exclusion of type specimens that are currently considered to be invalid does not alter conclusions concerning the absence of a recent trend in type specimen completeness for sauropodomorphs.

Benton's work is based on dinosaurian taxa as a whole, whereas the current dataset is restricted to sauropodomorphs; therefore, the differences in conclusions might reflect peculiarities of the taxonomy in the latter group compared to theropods and ornithischians. If this is correct, then trends that hold true for Ornithischia and Theropoda might overwhelm a separate and different signal from the sauropodomorphs. There is one peculiarity of derived sauropods that potentially might have enabled the erection of more taxa based on fragmentary remains in comparison to

other dinosaurs; this is the complexity of their presacral vertebrae which may mean that a single dorsal is diagnostic. However, basal sauropodomorphs and non-eusauropods do not possess complex laminae and it should be noted that many theropods also possess moderately complex laminae (Wilson 1999; Weishampel *et al*. 2004b, and references therein). The possibility that the quality of sauropodomorph type material has differed through historical time relative to that for ornithischians and theropods could be tested by partitioning Benton's dinosaurian data into subsets pertaining to these three clades. Unfortunately, Benton's data could not be partitioned in this way because his dataset does not provide a breakdown of type species numbers and quality scores beyond the level of Dinosauria. Of note, however, is that throughout the history of the study and naming of dinosaurs, many of the individual workers who have erected new sauropodomorph taxa have worked on a broad range of dinosaurs, encompassing all three major clades. It seems unlikely that these workers, and those of today, have applied inconsistent standards when dealing with different groups. This view is consistent with the observation, noted above, that the trend toward increasing type specimen completeness disappears for Dinosauria as a whole when Benton's dataset is re-analysed for more recent time periods. There is one additional factor that may possibly bias theropods in terms of increasing preservation potential with time. This relates to the relatively recent discovery of taxa of extremely small body size which may be affected by different taphonomic processes than other large-bodied dinosaurs. However, large theropods have also been described in recent years and this effect cannot be used to explain ornithischian completeness either. Thus, pending a clade-by-clade analysis, the idea that the systematic practices applied to sauropodomorphs have been significantly different from those applied to theropods and ornithischians is provisionally rejected.

Is taxonomic practice improving through time?

Poor average completeness of the type specimens of the earliest named taxa is expected because early workers had less material upon which to make comparisons: thus new specimens would frequently appear to be unique and only with subsequent discoveries would 'diagnostic' features be shown to be 'historically obsolescent' (Wilson and Upchurch 2003). In contrast, modern workers have a wealth of comparative data, making it easier to recognise that a fragmentary specimen cannot be uniquely diagnosed as a new genus or species. The absence of a more recent trend towards increased type specimen quality is a more complex issue. It seems self-evident that our knowledge of the dinosaurian fossil record is vastly superior today, and that many recently discovered taxa have been based on exquisitely preserved and very complete material, often including multiple individuals. For example, prior to the 1970s, the average number of sauropodomorph genera named per decade was less than four, rising to 13 and 12 new genera in the 1970s and 1980s respectively. From 1990 onwards, there has been an exponential increase (Figure 5.3), with 31 named in the 1990s and already 71 named in the 2000s (accounting for 40% of all named sauropodomorph taxa). Under such circumstances, the relatively low completeness scores for recently described type specimens seem paradoxical. However, it should be noted that the current data (and that of Benton [2008a, b]) are based on virtually comprehensive lists of type specimens and therefore includes not only spectacular nearly complete skeletons and skulls, but also all type specimens based on isolated fragments. Thus, overall completeness scores for recent decades might be lowered because palaeontologists continue to name new taxa on the basis of very fragmentary specimens such as isolated teeth or vertebrae. This explanation is supported by both the current data on sauropodomorphs and also that of Benton (2008a) for dinosaurs as a whole. For example, the current dataset indicates that this decade has one of the lowest average completeness scores. This is because, although relatively complete taxa such as *Unaysaurus* (SCM_{ts} = 48%, CCM_{ts} = 56%) and *Pantydraco* (SCM_{ts} = 45%, CCM_{ts} = 60%)

have been named this decade, numerous other taxa have been erected based on very fragmentary and incomplete material (e.g. *Xenoposeidon* [SCM_{ts} = 1%, CCM_{ts} = 6%], *Borealosaurus* [SCM_{ts} = 1%, CCM_{ts} = 3%] and *Nopcsaspondylus* [SCM_{ts} = 1%, CCM_{ts} = 7%]). Benton (2008b: table 1, supplementary materials) lists the number of type specimens in each time bin cohort for each of his five quality categories. Although the emphasis is upon the increasing number of type specimens with quality scores of 2-5 through time, the data also demonstrate an increase in type specimens with quality scores of 1: the three most recent cohorts (1990-1994, 1995-1999 and 2000-2004) all contain more type specimens with a quality score of 1 than any preceding five-year time bin, with the exception of 1875-1879.

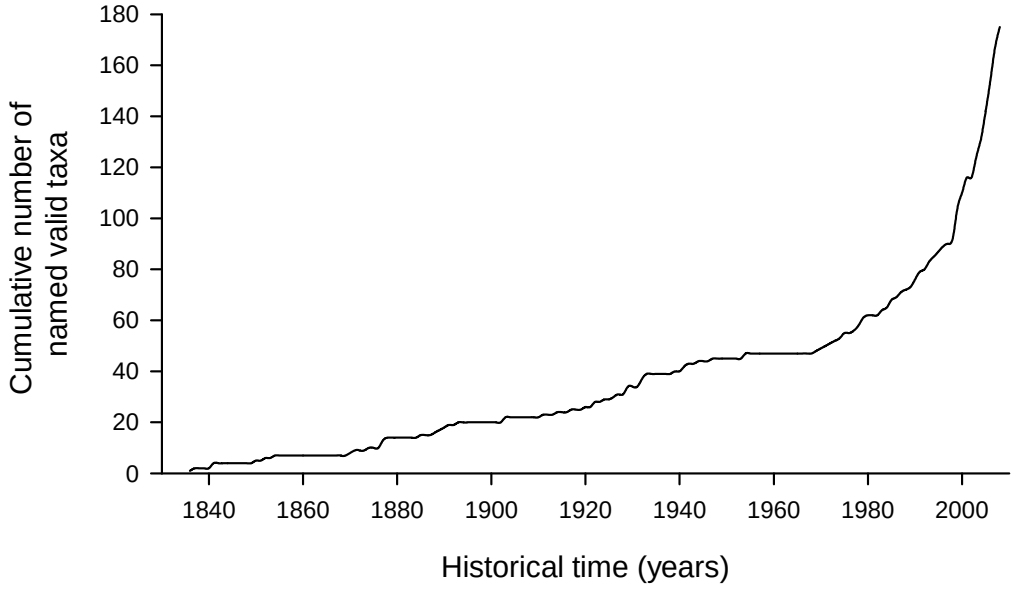

FIGURE 5.3. Collector curve showing cumulative number of sauropodomorph taxa named through historical time.

Benton (2008a: p.1) noted several reasons why palaeontologists might be tempted to name new dinosaurian taxa on the basis of fragmentary material:

‘Dinosaurs have been subject to intense study over the past 200 years, and never more so than at present. There is a risk, however, that systematists might be tempted to name new species on the basis of incomplete and undiagnostic materials, particularly if the group is of intense public interest, and there is a career premium in naming new species….It could be that palaeontologists are producing poor-quality work, perhaps fuelled in part by excessive interest from museums and the media worldwide. There is a risk that undue pressure from funding agencies, or even from scientific journals, might lead palaeontologists to name new species when they do not feel a new name is warranted: it is well known, for example, that the press prefers a story about a ‘new species of dinosaur’, rather than another example of a previously named form.’

The premises that relative completeness equates to type specimen quality, and that new taxa should be erected on the basis of high quality (and therefore relatively complete) material, deserve evaluation. First, as noted previously, the completeness of a specimen does not entirely correlate with its taxonomic or phylogenetic informativeness. This is because the number of phylogenetically informative character states varies between taxa and across different regions of the skeleton. Related to this is the distribution of autapomorphies; for example, the sauropods *Barosaurus* (SCM2 = 65%, CCM2 = 56%) and *Omeisaurus* (SCM2 = 98%, CCM2 = 100%) are currently known to possess only three and six autapomorphies respectively (Wilson 2002; Upchurch *et al*. 2004a). This contrasts with *Xenoposeidon* from the Early Cretaceous of the UK, which is based on a single incomplete dorsal vertebra (SCM_{ts} = 1%, CCM_{ts} = 6%) and yet apparently possesses six autapomorphies (Taylor and Naish 2007). Of course, the fact that the six autapomorphies of *Xenoposeidon* are restricted to a single dorsal vertebra, whereas the six pertaining to *Omeisaurus* are distributed widely across its skeleton, might mean that the former taxon is more prone to historical obsolescence than the latter. Nevertheless, it seems probable that the ‘quality’ of a type specimen, in terms of its longevity as a valid taxon, is not merely a function of its completeness; rather it may depend on a complex mix of completeness and information content.

A second factor is that some workers have argued that the failure to name very fragmentary, but potentially diagnosable, specimens leads to biases in studies of diversity patterns (Naish and Martill 2007; Taylor and Naish 2007). Because such specimens lack a name, they tend to be ignored in diversity studies which collect data on the numbers of genera or species through time (see Chapter 4). Another benefit of naming fragmentary, but diagnosable, specimens is that they tend to attract more attention from systematists than material labelled, for example, as 'Sauropoda indet.' Named taxa are therefore more likely to take part in taxonomic, phylogenetic and biogeographic studies.

The results demonstrate that there is no discernible increase in the completeness of dinosaurian type specimens through most of historical time to the present day. This is because, whether for non-scientific reasons (e.g. self-promotion) or scientific ones (e.g. diversity estimation), palaeontologists continue to name taxa on very incomplete specimens as well as very complete ones. This practice probably persists because of a complex mixture of motives, including the less desirable ones listed by Benton (2008a, b), as well as the more laudable scientific objectives outlined above. To suggest that dinosaurian type specimen quality is better now than in the past is not borne out by current data, and even if it were, such a statement would seem to be an oversimplification.

(3) Completeness metrics in a wider context

In principle, the completeness metrics could be modified for use with other vertebrates, or even non-vertebrate groups. Such metrics are more 'fine-grained' and less arbitrary than simple quality scales based on five or six broad categories. Below, the potential advantages and disadvantages of the variants of SCM and CCM are briefly discussed (since this may affect decisions regarding which one is most appropriate for a particular study), as well as the potential role of completeness metrics in the study of diversity patterns.

The costs and benefits of different completeness metrics

In general, the results indicate that SCM1, SCM2, CCM1 and CCM2 behave in a very similar way to each other (Figs. 5.1 and 5.2; Tables 5.1 and 5.3; $p < 0.001$ for all tests). This suggests that the choice of completeness metric, and the percentages awarded to different parts of the skeleton, do not make a critical difference to conclusions concerning the completeness of the sauropodomorph fossil record through either geological or historical time. Nevertheless, the current work represents just a single set of case studies based on sauropodomorphs, and the consistent performance of the various metrics may not hold true in other contexts or when applied to other groups.

In principle, CCM is preferred to SCM because the percentage weights given to each part of the skeleton are dictated by the detailed evaluation of the distribution of anatomical characters in phylogenetic studies. The percentages used in the CCM therefore appear to be less arbitrary than those applied in the SCM. However, both SCM and CCM have been applied because each is designed to capture slightly different aspects of preservation in the fossil record. SCM attempts to capture a combination of the number of elements preserved and their physical bulk. Such a metric may be most useful in taphonomic studies (see Chapter 8) when, for example, workers wish to quantify and

compare the amount of material preserved in a series of individuals from different localities, facies or horizons, although it should be noted that there are problems with using it for taphonomic analyses (see 'Chapter Two'). CCM attempts to capture information on the taxonomic/phylogenetic information content of each specimen and may therefore be particularly suited to the study of diversity patterns through geological time (see below) and trends in systematics through historical time. CCM also has the benefit over SCM and Benton's (2008a, b) metrics in that it does not over-score poorly preserved, but complete, skulls, because it only scores the number of characters the skull can actually be coded for.

In general, SCM2 and CCM2 appear to be more useful measures than SCM1 and CCM1. This is partly because SCM2 and CCM2 can include information from many individuals, thereby allowing taxa such as bonebed-based forms (e.g. *Lapparentosaurus* and *Barapasaurus*) to be included (see 'Materials and Methods'). However, this strength of SCM2 and CCM2 is also a potential weakness: incorrect scores are more probable with these metrics because they rely more heavily on beliefs about the association of elements or the taxonomic affinities of individuals.

There is also a potential problem associated with the use of averaged completeness scores as a way of comparing different geological or historical time bins (see below).

Completeness metrics as sampling proxies?

A number of recent studies have raised concerns that the diversity fluctuations observed in the fossil record might, at least in part, be artefacts of sampling (Peters and Foote 2002; Peters 2005, 2008; Smith and McGowan 2007; see also Chapter 2). This has led to the development of several methods for measuring fossil record quality (e.g. Benton *et al*. 2000; Pol and Norell 2006; Wills *et a*l. 2008), removal of biases via rarefaction (e.g. Raup 1975), and the use of sampling proxies (e.g. Upchurch and Barrett

2005; Barrett *et al*. 2009; Butler *et al*. 2009). The completeness metrics proposed here could be added to the growing list of sampling proxies, which currently includes numbers of fossil-bearing geological formations (e.g. Upchurch and Barrett 2005; Butler *et al*. 2009), numbers of collections or localities sampled (e.g. Crampton *et al*. 2003; Alroy *et al*. 2008), and sedimentary rock outcrop area (e.g. Peters and Foote 2002; Peters 2005; Smith and McGowan 2007).

The principle underlying the use of sampling proxies is that there should be some mechanism by which the proxy controls opportunities to observe diversity in the fossil record. For example, sedimentary rock outcrop area could affect observed diversity because the amount of rock preserved during each time bin has some control over the number of opportunities to collect fossils. It is unlikely, however, that any single proxy will represent all of the diverse factors that might produce sampling biases (see Chapters 2 and 4). One aspect of observed diversity that is not captured by previous sampling proxies relates to how the state of preservation of fossils controls opportunities to identify particular genera or species. A time bin might contain a relatively large amount of sedimentary rock including numerous formations, and might also have been thoroughly sampled in terms of the number of localities visited and the number of collections made, but observed diversity will still be low if the recovered fossils are so fragmentary that they can only be assigned to indeterminate members of a higher taxa. The ability to identify fossils to lower taxonomic levels, such as genus or species, depends on which parts of the organism are preserved and the taxonomic/phylogenetic information content of those parts. Therefore, completeness metrics, especially the CCM, could provide an additional sampling proxy for use in studies of palaeodiversity patterns. If a correlation between a completeness metric and observed diversity does not occur, this might be because of anomalous effects, such as those outlined above relating to taxonomic practice, but whatever the reason for the lack of correlation, this will show that completeness is not acting as a control and can be ignored further in a diversity study. However, if a correlation between observed

diversity and a completeness metric is found (as is the case for sauropods in the Cretaceous), then the effects of fluctuations in preservation quality through time should be evaluated and removed in order to obtain a more accurate reconstruction of diversity patterns.

CHAPTER SIX

PALAEOLATITUDINAL PATTERNS

Analyses and Results

Analyses have been implemented to look for any indication of palaeolatitudinal patterns in sauropod and ornithischian distribution. Sauropod body fossil and tracksite distribution has been compared with ornithischian tracksites. Tracksites and tracksite regions have both been analysed. The ornithischian element of the Cretaceous dataset of Butler and Barrett (2008), which includes tracksites and body fossils, has been utilised as a further comparison. In addition, taxic diversity of sauropodomorphs and ornithischians has also been used. The use of sauropodomorphs, rather than Sauropoda, in the diversity study enables the investigation of Late Triassic patterns. The potential effects of sampling biases are then explored and the results of the residuals reported.

All palaeolatitudinal curves (as well as DBCs) display statistically significant *p*-values ($W > 0.28$; $p < 0.001$) when tested for normality, meaning that a normal distribution can be rejected. Statistical comparisons between curves are reported in Table 6.1.

Abundance distribution

Total evidence

The vast majority (92%) of sauropod tracksites are known from the Northern Hemisphere. Tracksites are known from 0-50° either side of the Equator, although the majority (89%) are restricted to 20-50° N, with the mean average Northern Hemisphere palaeolatitude being 35° N (the mean average Southern Hemisphere palaeolatitude is closer to the Equator [26° S]). When only tracksite regions are considered, similar values are recovered (mean averages of 32° N and 26° S). These mean average palaeolatitudes are slightly higher than those recorded by Lockley *et al*. (1994) and reflect an increasing number of sites known from countries such as the Republic of Korea and the USA (Foster and Lockley 2006; Lockley *et al*. 2006). The mean average palaeolatitudes for

sauropod body fossils (based on numbers of individuals and localities) are 33° N and 34-35° S, with body fossils known up to 53° N and as far South as 70° S.

As with sauropods, Northern Hemisphere locations dominate the ornithischian tracksite record (92%). However, ornithischians are known from a wider range of palaeolatitudes than sauropods: 0-83° N and 0-60° S. The majority, though, are restricted to 30-50° N, with the mean average palaeolatitude for the Northern Hemisphere being 40° N (the mean average Southern Hemisphere palaeolatitude is 23° S). When Cretaceous ornithischian body fossils (using numbers of individuals and localities from the Cretaceous dataset of Butler and Barrett [2008]) are considered, however, these average values differ from the tracksite data, particularly for the Southern Hemisphere (45° N and 53-55° S).

Temporal variation

For the Early-Middle Jurassic the mean average palaeolatitude of sauropod tracksites in the Northern Hemisphere is 28° N. The average palaeolatitude moves northwards in the Late Jurassic (35° N) and again in the Early Cretaceous (38° N). Mean average palaeolatitude for the Late Cretaceous returns to Early-Middle Jurassic levels (29° N). When tracksite regions are considered, mean average palaeolatitudes for the Northern Hemisphere show similar temporal fluctuations: 28° N (Early-Middle Jurassic), 34° N (Late Jurassic), 35° N (Early Cretaceous) and 28° N (Late Cretaceous). Sauropod body fossil data (using numbers of individuals and localities) vary slightly from the tracksite averages: 34-36° N (Early-Middle Jurassic), 35° N (Late Jurassic), 30° N (Early Cretaceous) and 32° N (Late Cretaceous).

Ornithischian tracksites show a slightly different temporal pattern to that of sauropods. In the Early-Middle Jurassic, the mean average palaeolatitude for the Northern Hemisphere is 31° N, with this rising to 35° N in the Late Jurassic. These values are fairly

similar to the mean averages for sauropods. However, average palaeolatitudes for the Early Cretaceous (43° N) and Late Cretaceous (51° N) are considerably more northerly. Additionally, when tracksite regions are analysed, Northern Hemisphere mean average palaeolatitudes still show similar (though slightly more southerly) temporal fluctuations: 32° N (Early-Middle Jurassic), 34° N (Late Jurassic), 39° N (Early Cretaceous) and 45° N (Late Cretaceous). Furthermore, the Cretaceous dinosaurian dataset of Butler and Barrett (2008) shows similar average palaeolatitudes for Northern Hemisphere ornithischian tracksites for the Early Cretaceous (42° N) and Late Cretaceous (47° N). Body fossil data (using individuals and localities) from the Butler and Barrett (2008) study also show comparable average palaeolatitudes: 38-39° N for the Early Cretaceous and 47° N for the Late Cretaceous. This Cretaceous change in average palaeolatitudes seems to explain the differences in datasets noted above.

Rees *et al*. (2004) noted that Late Jurassic plant diversity is highest between 40-50° N with the peak in dinosaur diversity slightly further southward (30-40° N). This same palaeolatitudinal peak in abundance (30-40° N) is noted here for Late Jurassic sauropod and ornithischian tracksites and body fossils.

Diversity distribution

When sauropodomorph taxic diversity is considered in its entirety, the average palaeolatitudes for the two hemispheres are 32° N and 39° S. Ornithischian taxic diversity, in contrast, peaks much more poleward, with mean average palaeolatitudes of 43° N and 50° S. When the distribution of these two clades is compared through time, sauropodomorph diversity in the Northern Hemisphere peaks at a fairly constant mean average palaeolatitude of 30-34° N (although Southern Hemisphere palaeolatitudes tend to be somewhat closer to the pole). Mean average peaks in ornithischian diversity display approximately the same palaeolatitudinal patterns (including the more poleward

Southern Hemisphere palaeolatitudes), but departs from this to some extent in the Early Cretaceous (39° N and 64° S) and entirely in the Late Cretaceous (47° N and 46° S).

Palaeolatitudinal sampling biases

Abundance

Use of 5° and 10° palaeolatitudinal bins results in the same patterns and will not be discussed separately. Nearly all of the palaeolatitudinal abundance data show a statistically strong positive correlation with DBCs ($p < 0.001$), suggesting that sampling biases are exerting a prominent influence on sauropod and ornithischian distribution (Table 6.1). Strong statistical support exists for a positive correlation between sauropod body fossils (for both individuals and localities) and tracksites (including tracksite regions) for the Jurassic and Early Cretaceous; this support is still present in the Late Cretaceous, although the correlation is much weaker. For Ornithischia, there is no correlation between tracksites and DBCs in the Early-Middle Jurassic (note that it has not been possible to test for Jurassic ornithischian body fossils), but a moderately strong correlation is present in the Late Jurassic. In the Early Cretaceous there is a strong correlation between body fossils and tracksites (with the exception of tracks from the Cretaceous dataset of Butler and Barrett 2008) and DBCs, and this is retained (albeit with a slightly weaker correlation) in the Late Cretaceous.

A: *10° bins*	**EJ**	**LJ**	**EK**	**LK**
S tracksites	rs=0.5952 (*p*=0.013); tau=0.5062 (*p*=0.011)	rs=0.5631 (*p*=0.017); tau=0.4841 (*p*=0.017)	rs=0.8261 (*p*<0.001); tau=0.6887 (*p*<0.001)	rs=0.4606 (*p*=0.050); tau=0.3595 (*p*=0.068)
S track regions	rs=0.5719 (*p*=0.013); tau=0.4819 (*p*=0.008)	rs=0.5631 (*p*=0.016); tau=0.4841 (*p*=0.013)	rs=0.8443 (*p*<0.001); tau=0.7330 (*p*<0.001)	rs=0.4724 (*p*=0.039); tau=0.3973 (*p*=0.035)
S fossil individuals	rs=0.8261 (*p*<0.001);	rs=0.9039 (*p*<0.001);	rs=0.8873 (*p*<0.001);	rs=0.5943 (*p*=0.010);

	tau=0.6708 (*p*<0.001)	tau=0.8200 (*p*<0.001)	tau=0.7487 (*p*<0.001)	tau=0.4728 (*p*=0.007)
S fossil localities	rs=0.8578 (*p*<0.001); tau=0.7213 (*p*<0.001)	rs=0.9039 (*p*<0.001); tau=0.8200 (*p*<0.001)	rs=0.8814 (*p*<0.001); tau=0.7404 (*p*<0.001)	rs=0.6062 (*p*=0.002); tau=0.4815 (*p*=0.002)
O tracksites	rs=0.3551 (*p*=0.162); tau=0.3045 (*p*=0.151)	rs=0.6653 (*p*=0.004); tau=0.5756 (*p*=0.002)	rs=0.8156 (*p*<0.001); tau=0.6671 (*p*<0.001)	rs=0.5856 (*p*=0.020); tau=0.4517 (*p*=0.025)
O track regions	rs=0.3498 (*p*=0.156); tau=0.2848 (*p*=0.165)	rs=0.6674 (*p*=0.004); tau=0.5913 (*p*<0.001)	rs=0.8091 (*p*<0.001); tau=0.6623 (*p*<0.001)	rs=0.6154 (*p*=0.009); tau=0.4811 (*p*=0.012)
O tracks (B)	N/A	N/A	rs=0.4336 (*p*=0.067); tau=0.3073 (*p*=0.104)	rs=0.6678 (*p*=0.003); tau=0.5586 (*p*=0.001)
O fossil individuals (B)	N/A	N/A	rs=0.7784 (*p*=0.001); tau=0.6260 (*p*=0.001)	rs=0.5495 (*p*=0.014); tau=0.4003 (*p*=0.018)
O fossil localities (B)	N/A	N/A	rs=0.7417 (*p*=0.001); tau=0.5686 (*p*=0.001)	rs=0.5638 (*p*=0.014); tau=0.4327 (*p*=0.013)

B: *5° bins*	**EJ**	**LJ**	**EK**	**LK**
S tracksites	rs=0.6328 (p<0.001); tau=0.5511 (p<0.001)	rs=0.5889 (p<0.001); tau=0.5284 (p<0.001)	rs=0.6130 (p<0.001); tau=0.5188 (p<0.001)	rs=0.4220 (p=0.009); tau=0.3500 (p=0.007)
S track regions	rs=0.6206 (p<0.001); tau=0.5332 (p<0.001)	rs=0.5889 (p<0.001); tau=0.5284 (p<0.001)	rs=0.6169 (p<0.001); tau=0.5265 (p<0.001)	rs=0.4168 (p=0.006); tau=0.3403 (p=0.007)
S fossil individuals	rs=0.7673 (p<0.001); tau=0.6611 (p<0.001)	rs=0.8338 (p<0.001); tau=0.7526 (p<0.001)	rs=0.7790 (p<0.001); tau=0.6576 (p<0.001)	rs=0.6529 (p<0.001); tau=0.5405 (p<0.001)
S fossil localities	rs=0.7792 (p<0.001); tau=0.6829	rs=0.8338 (p<0.001); tau=0.7526	rs=0.7823 (p<0.001); tau=0.6670	rs=0.6557 (p<0.001); tau=0.5415

	(p<0.001)	(p<0.001)	(p<0.001)	(p<0.001)
O tracksites	rs=0.3691 (p=0.029); tau=0.3282 (p<0.023)	rs=0.6176 (p<0.001); tau=0.5492 (p<0.001)	rs=0.7422 (p<0.001); tau=0.6215 (p<0.001)	rs=0.4994 (p=0.004); tau=0.3861 (p=0.004)
O track regions	rs=0.3678 (p=0.028); tau=0.3214 (p=0.024)	rs=0.6181 (p<0.001); tau=0.5539 (p<0.001)	rs=0.6896 (p<0.001); tau=0.5782 (p<0.001)	rs=0.5306 (p=0.005); tau=0.4352 (p=0.005)
O tracks (B)	N/A	N/A	rs=0.4518 (p=0.006); tau=0.3691 (p=0.005)	rs=0.5932 (p<0.001); tau=0.4881 (p<0.001)
O fossil individuals (B)	N/A	N/A	rs=0.7177 (p<0.001); tau=0.5836 (p<0.001)	rs=0.5892 (p=0.001); tau=0.4641 (p=0.001)
O fossil localities (B)	N/A	N/A	rs=0.7056 (p<0.001); tau=0.5803 (p<0.001)	rs=0.6269 (p<0.001); tau=0.5137 (p<0.001)

TABLE 6.1. Results of statistical comparisons between sauropod and ornithischian abundance and numbers of dinosaur-bearing collections. (A) Results of comparisons using 10° palaeolatitudinal bins; (B) Results of comparisons using 5° palaeolatitudinal bins. EJ=Early-Middle Jurassic; LJ=Late Jurassic; EK=Early Cretaceous; LK=Late Cretaceous; S=sauropods; O=ornithischians; rs=Spearman's rank; tau=Kendall's tau.

Diversity

Palaeolatitudinal patterns of sauropodomorph taxic diversity are strongly correlated ($p < 0.001$) with DBCs (using both 5° and 10° bins), with this correlation particularly strong for the Jurassic (Table 6.2). Ornithischian diversity also closely matches DBCs, although this correlation is fairly weak for the Late Triassic; this is likely, however, to be the result of just three valid taxa currently known from this interval.

	LT	EJ	LJ	EK	LK
S (10° bins)	rs=0.6506 (*p*=0.003); tau=0.5575 (*p*=0.004)	rs=0.8421 (*p*<0.001); tau=0.7291 (*p*<0.001)	rs=0.8282 (*p*<0.001); tau=0.7452 (*p*<0.001)	rs=0.7194 (*p*=0.001); tau=0.5774 (*p*=0.001)	rs=0.6975 (*p*=0.001); tau=0.5948 (*p*=0.001)
S (5° bins)	rs=0.5620 (*p*<0.001); tau=0.5234 (*p*<0.001)	rs=0.7090 (*p*<0.001); tau=0.6231 (*p*<0.001)	rs=0.7135 (*p*<0.001); tau=0.6537 (*p*<0.001)	rs=0.6634 (*p*<0.001); tau=0.5374 (*p*<0.001)	rs=0.5883 (*p*<0.001); tau=0.4978 (*p*<0.001)
O (10° bins)	rs=0.4300 (*p*=0.046); tau=0.3876 (*p*=0.046)	rs=0.7137 (*p*<0.001); tau=0.5715 (*p*<0.001)	rs=0.7293 (*p*<0.001); tau=0.6248 (*p*<0.001)	rs=0.6038 (*p*=0.007); tau=0.4772 (*p*=0.008)	rs=0.7186 (*p*=0.003); tau=0.6117 (*p*=0.001)
O (5° bins)	rs=0.3880 (*p*=0.020); tau=0.3514 (*p*=0.020)	rs=0.6043 (*p*<0.001); tau=0.5280 (*p*<0.001)	rs=0.6675 (*p*<0.001); tau=0.5949 (*p*<0.001)	rs=0.6164 (*p*=0.001); tau=0.5167 (*p*<0.001)	rs=0.7220 (*p*<0.001); tau=0.6247 (*p*<0.001)

TABLE 6.2. Results of statistical comparisons between sauropodomorph and ornithischian diversity and numbers of dinosaur-bearing collections. See Table 6.1 for abbreviations (except for 'S' which stands for 'sauropodomorphs' here).

Residuals - abundance

After correcting for sampling bias, sauropod abundance displays peaks at 0-10° N and 20-30° N (with a smaller peak at 10-20° S) in the Early-Middle Jurassic, with abundance low at 20-50° S (Fig. 6.1). Ornithischian abundance shows almost the exact same pattern (Fig. 6.1), with the exceptions being low abundance at 30-40° N and high abundance at 40-50° N (both palaeolatitudes at which sauropod abundance appears largely controlled by the number of DBCs).

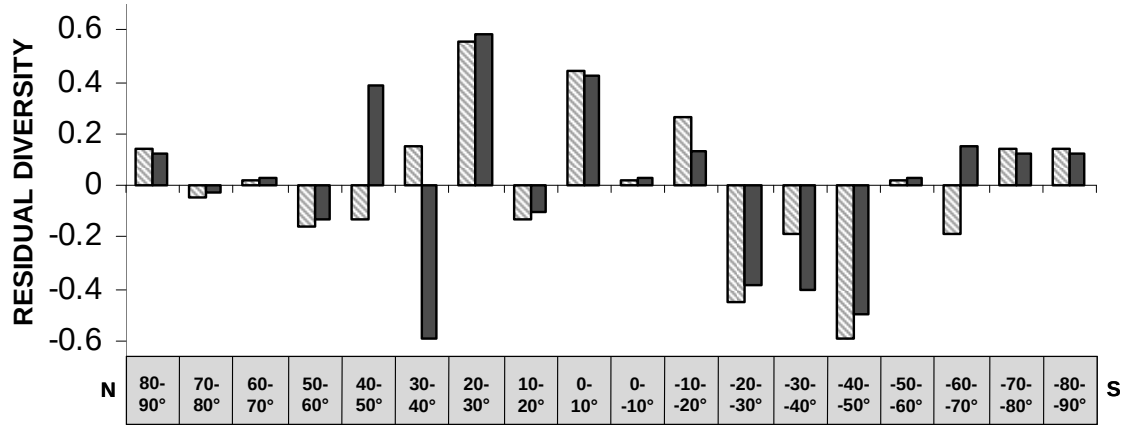

FIGURE 6.1. DBC-based residuals for sauropod (diagonal lines) and ornithischian (solid bars) tracksite abundance for the Early-Middle Jurassic.

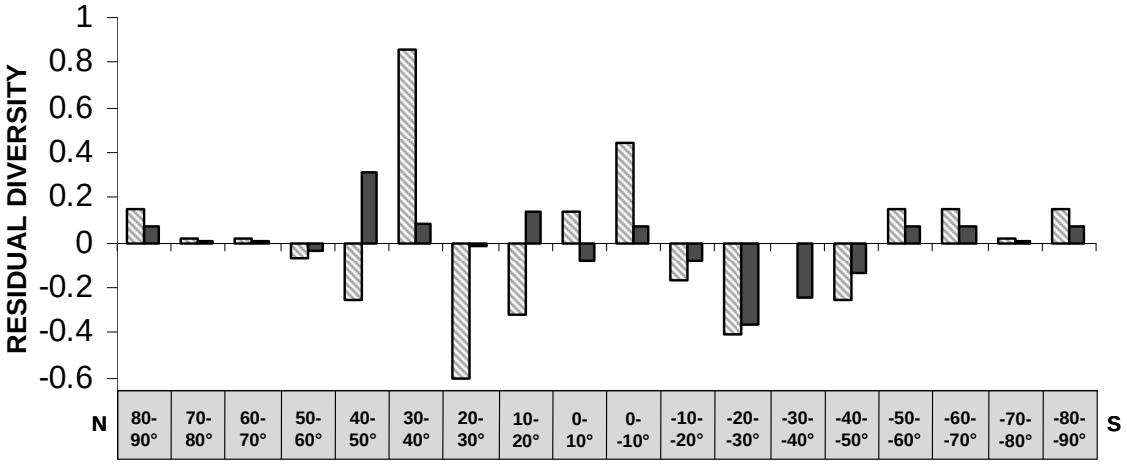

FIGURE 6.2. DBC-based residuals for sauropod (diagonal lines) and ornithischian (solid bars) tracksite abundance for the Late Jurassic.

In the Late Jurassic, the peak in sauropod abundance occurs at 30-40° N, with another smaller peak at 0-10° S (Fig. 6.2). Sauropod abundance is notably low at 20-30° N, with other shallower troughs present at 10-20° N, 40-50° N and 20-30° S. Ornithischian abundance appears largely controlled by sampling, although there is a peak at 40-50° N and a trough at 20-30° S (Fig. 6.2).

Peaks in sauropod abundance in the Early Cretaceous are present at 20-30° N, 40-50° N and 80-90° S, with smaller peaks also present at 70-90° N. There are troughs in sauropod abundance at 0-20° N, 50-60° N and 60-80° S (Fig. 6.3). Ornithischians share several of these peaks and troughs but differ most notably in that abundance is extremely high at 50-60° N (and moderately so at 30-40° N) and very low at 20-30° N (Fig. 6.3).

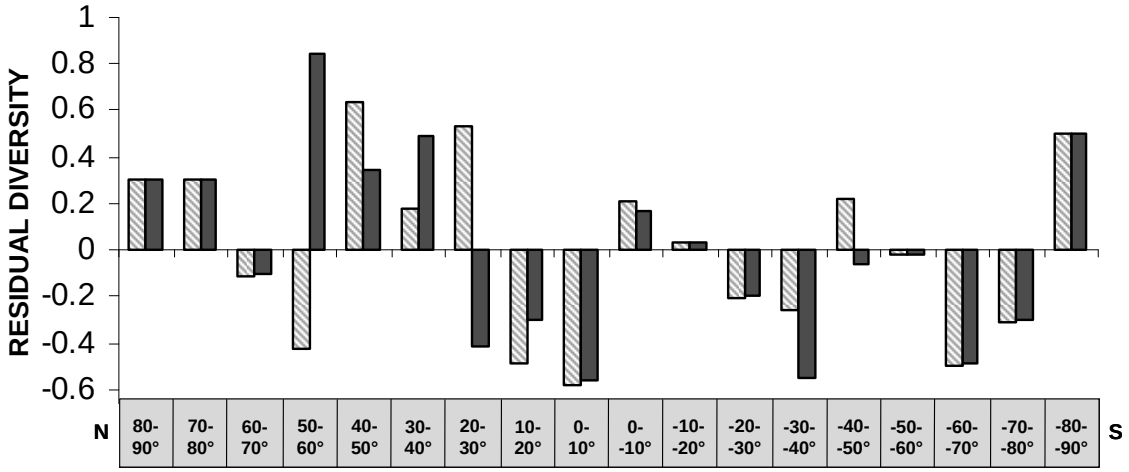

FIGURE 6.3. DBC-based residuals for sauropod (diagonal lines) and ornithischian (solid bars) tracksite abundance for the Early Cretaceous.

In the Late Cretaceous, sauropod abundance is highest at 10-40° N (with smaller peaks at 20-30° S and 70-90° S), while abundance is low at 40-60° N and 40-50° S (Fig. 6.4). The peak in ornithischian abundance, however, occurs at 60-70° N (with smaller peaks at 80-90° N, 10-20° S and 70-90° S), while troughs in abundance are present at 0-20° N, 50-60° N and 30-40° S (Fig. 6.4).

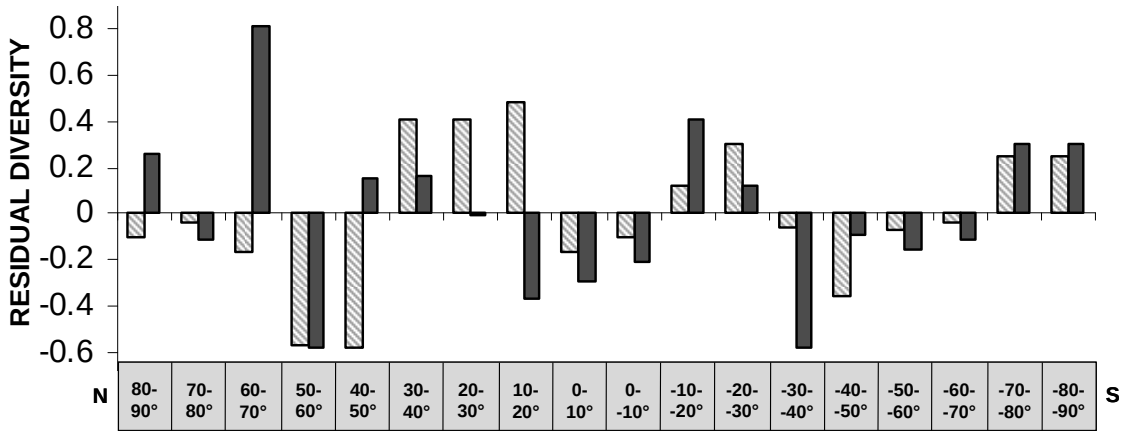

FIGURE 6.4. DBC-based residuals for sauropod (diagonal lines) and ornithischian (solid bars) tracksite abundance for the Late Cretaceous.

Residuals – diversity

In the Late Triassic, sauropodomorph diversity is demonstrated to be high at 30-40° N and 30-60° S and low at 0-30° N and 40-50° N (Fig. 6.5). Ornithischian diversity shows a similar pattern (with the exception of 40-50° S, where there is a small trough), although these peaks and troughs are less prominent (Fig. 6.5).

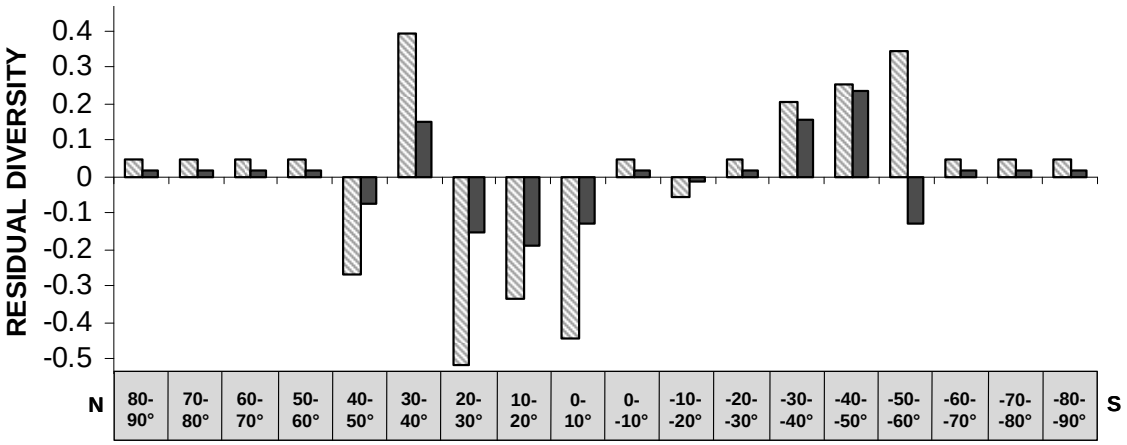

FIGURE 6.5. DBC-based residuals for sauropodomorph (diagonal lines) and ornithischian (solid bars) taxic diversity for the Late Triassic.

Sauropodomorph diversity in the Early-Middle Jurassic displays notable peaks at 20-40° N, 50-60° N and 50-60° S, with smaller peaks at 0-10° N, 80-90° N, 30-40° S and 70-90° S, while diversity is low for this clade at 10-20° N, 40-50° N and 10-30° S (Fig. 6.6). Ornithischian diversity shares a number of these peaks and troughs, but there are some notable differences. Diversity is high at 40-50° N and S, whereas sauropodomorph diversity is low at both these palaeolatitudes; similarly, ornithischian diversity is low at 20-30° N and 30-40° S, while there are peaks in sauropodomorph diversity for these same palaeolatitudes (Fig. 6.6).

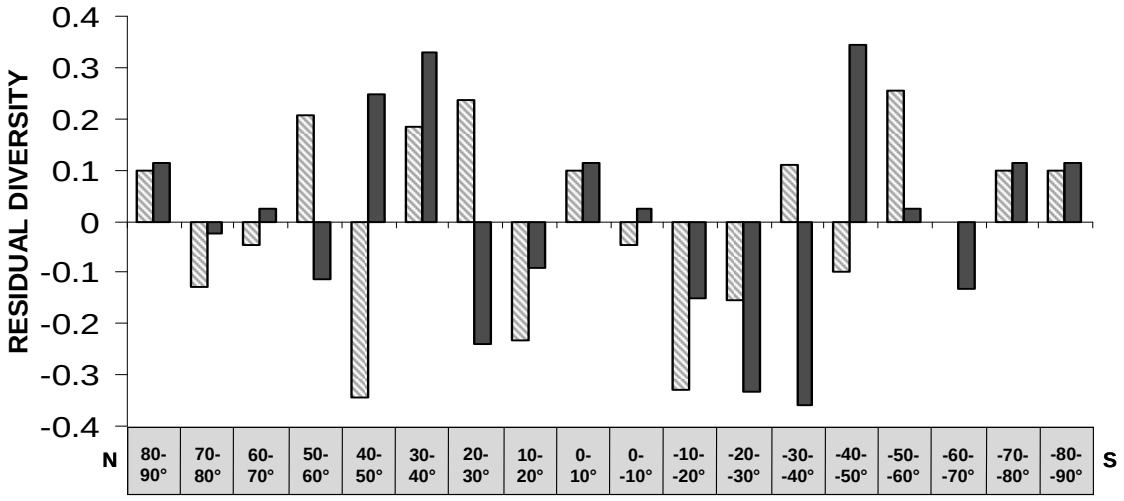

FIGURE 6.6. DBC-based residuals for sauropodomorph (diagonal lines) and ornithischian (solid bars) taxic diversity for the Early-Middle Jurassic.

In the Late Jurassic, sauropodomorph diversity is only shown to have had a prominent peak at 30-40° N, while there is a trough at 10-20° N (Fig. 6.7). Ornithischian diversity shows approximately the same patterns as sauropodomorph diversity, although there are peaks at 20-40° N and notable troughs at 10-20° N and 20-50° S (Fig. 6.7).

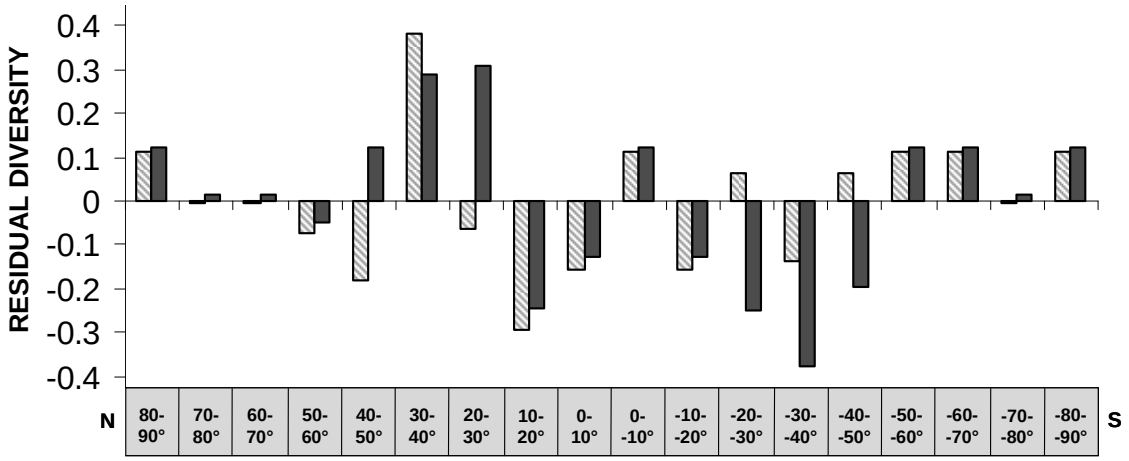

FIGURE 6.7. DBC-based residuals for sauropodomorph (diagonal lines) and ornithischian (solid bars) taxic diversity for the Late Jurassic.

Peaks in sauropodomorph diversity in the Early Cretaceous are restricted to 30-60° S and 80-90° S, while there are troughs at 50-60° N and 60-80° S (Fig. 6.8). Ornithischian diversity shows peaks at 30-50° N and 70-90° S, while there are troughs at 10-30° N, 50-60° N and 30-40° S (Fig. 6.8).

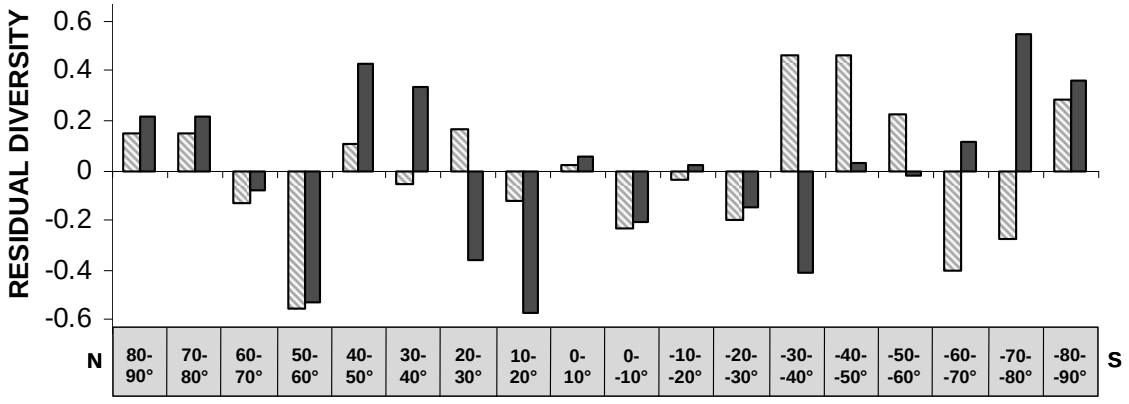

FIGURE 6.8. DBC-based residuals for sauropodomorph (diagonal lines) and ornithischian (solid bars) taxic diversity for the Early Cretaceous.

Sauropodomorph diversity in the Late Cretaceous shows a peak at 40-50° S, with lower peaks at 20-30° S and 70-90° S; there is a prominent diversity trough at 50-60° N (Fig.

6.9). Ornithischian diversity shows peaks at 30-60° N and 70-90° S, while diversity is low at 0-20° N and 20-40° S (Fig. 6.9).

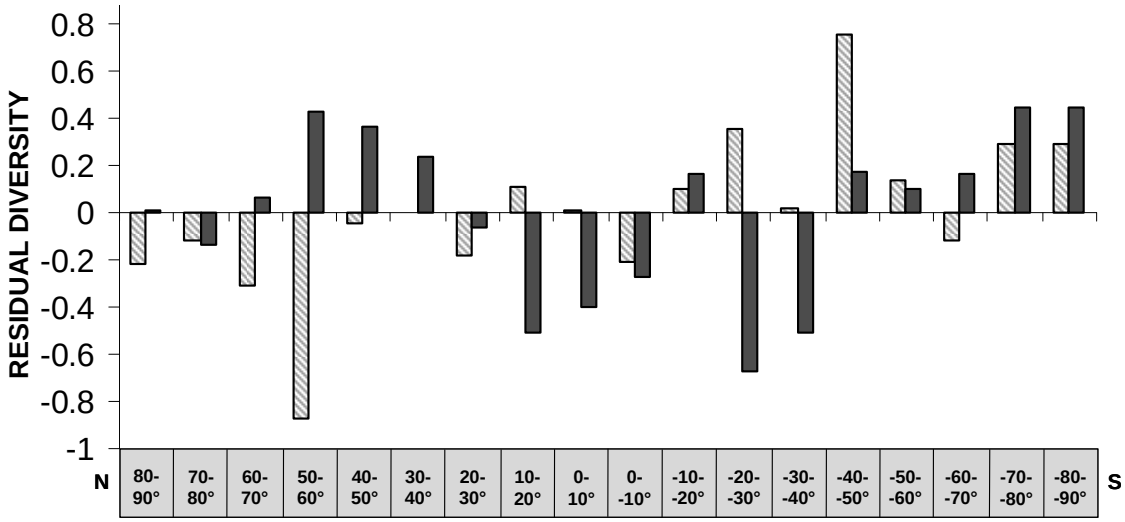

FIGURE 6.9. DBC-based residuals for sauropodomorph (diagonal lines) and ornithischian (solid bars) taxic diversity for the Late Cretaceous.

Discussion

The above results indicate that there were fluctuations in the palaeolatitudinal distribution of sauropodomorphs and ornithischians through time. However, more notably, it seems that sauropods and ornithischians occupied different average palaeolatitudes by the time of the Cretaceous, with this distributional skew particularly marked by the Late Cretaceous. This skew is supported by both the tracksite and body fossil abundance data (using the current dataset and that of Butler and Barrett 2008), as well as taxic diversity, suggesting that the two groups of herbivorous dinosaurs were beginning to live in different regions to one another by the Cretaceous. Butler and Barrett (2008) highlighted the possibility of some sort of habitat separation between sauropods and ornithischians during the Cretaceous and this hypothesis seems to be supported in the current analysis.

The effects of uneven sampling cannot be ruled out though, and the extent to which these patterns reflect the vagaries of the fossil record has also been investigated. The above results suggest that a large proportion of these palaeolatitudinal patterns are controlled by sampling biases, pertaining to collecting effort. An additional factor, not investigated here, that may play an important role in determining palaeolatitudinal patterns is the amount of land available for each time interval. The palaeocontinents were not distributed symmetrically with regards to the palaeoequator throughout the Mesozoic (Smith *et al*. 1994); therefore it is possible that some of the palaeolatitudinal peaks and troughs in diversity and abundance merely reflect the presence and absence, respectively, of land at these latitudes. For example, in the Late Jurassic many low latitude areas (particularly in the Northern Hemisphere) were covered with the Tethys Ocean, while there were large areas of land at high latitudes in the Southern Hemisphere (Smith *et al*. 1994; Scotese 2001). Thus, it might have been impossible for dinosaurs to be present at certain palaeolatitudes as a consequence of a lack of land.

Future studies could investigate this by calculating the amount of terrestrial land in each palaeolatitudinal bin and then using this as a sampling proxy.

Regardless of these sampling biases, however, the two clades do show different palaeolatitudinal patterns to one another, indicating that 'removal' of the effects of sampling (as has been attempted through the use of residuals) would still result in a distributional skew between sauropodomorphs and ornithischians. This suggests that the two clades did undergo some sort of palaeolatitudinal separation during the Cretaceous (Barrett and Butler 2008), with this skew becoming particularly prominent in the Late Cretaceous. Why this should be the case, however, remains uncertain. One possibility is this skew relates to environmental preferences. As was outlined in Chapter 3, most Late Cretaceous sauropods were titanosaurs and these animals displayed a preference for inland environments. However, the dominant Late Cretaceous ornithischians were hadrosaurids (which represent over 50% of all Late Cretaceous ornithischian occurrences: www.pbdb.org; Carrano 2008b) and Butler and Barrett (2008) demonstrated that this group showed a preference for coastal settings (ankylosaurs, which comprise over 15% of Late Cretaceous ornithischians, also show the same association). Thus, it is possible that these environmental preferences drove sauropods and ornithischians to inhabit different niches and therefore different palaeolatitudes. Other (or possibly related) possibilities might include the different dietary needs of the two groups. For example, if sauropods fed on plant X and ornithischians on plant Y, and X and Y occupied different palaeolatitudes, then it is likely that each dinosaur clade would also occupy a different palaeolatitude to one another. This could be tested by comparing floral distributions through the Mesozoic and examining these for correlations with dinosaur distribution. However, testing of this idea is seriously hampered by a lack of evidence for what dinosaurs actually ate, with only a very small number of fossils providing evidence for dinosaur diets. Additionally, previous comparisons between Cretaceous dinosaurs and plants have resulted in few

correlations in terms of diversity, abundance or distribution (Barrett and Willis 2001; Butler *et al*. 2009a, b).

A comparison between the LBGs of the two herbivorous clades and palaeoclimatic biome zones for the Late Cretaceous (Sellwood and Valdes 2006) reveals some interesting patterns. Sauropodomorph diversity is high in tropical ('summerwet') and humid climes, whereas ornithischians (although present in such regions) are largely restricted to warm ('winterwet') and cold temperate zones. A preference for different climatic zones, perhaps interlinked to floral distributions and the different dietary needs of the two groups (see above), may be an additional cause for their palaeolatitudinal habitat separation.

CHAPTER SEVEN

TRACKWAY ABUNDANCE

Analyses and Results

Sauropod tracksite abundance through time has been compared with ornithischian tracksite abundance, sauropod taxic diversity (TDE), proxies for the rock record (DBFs and rock outcrop area [Smith and McGowan 2007]), DBCs, specimen completeness and the sea level curve of Haq *et al*. (1987). These correlations have been tested in order to examine whether tracksite abundance is merely controlled by sampling and the effects of taphonomic biases, or if it reflects genuine fluctuations in sauropod abundance through time. The sampling proxies have also been compared with tracksite regional abundance, but these results are only reported separately where they differ from tracksite abundance.

Time-binning issues

One potential concern with attempts to analyse how tracksite abundance has fluctuated through time is that there is a greater period of time for tracksites to be preserved during longer time intervals; consequently, time periods of longer durations may contain higher numbers of tracksites merely because there has been a greater opportunity for them to be preserved. However, there is no correlation between substage duration and sauropod tracksite abundance (Spearman's $r_s = 0.211$; $p = 0.149$) for the Mesozoic, with the relatively short Kimmeridgian and Tithonian stages (each 4.9-5.3 Myr in duration) containing numbers of tracksites (46-50) an order of magnitude greater than that of the much longer Campanian (12.9 Myr in duration; 6-9 tracksites). This suggests that fluctuations in tracksite abundance are not merely the product of differences in time bin duration.

Sauropod tracksite abundance through time

Sauropod tracksite abundance remains low throughout the Early Jurassic and into the Middle Jurassic, before a small peak in the Bathonian (Fig. 7.1). Abundance then returns to pre-Bathonian levels in the Callovian-Oxfordian before a prominent peak in the Kimmeridgian-Tithonian. There is then a notable decline in the number of tracksites at the J/K boundary, although Early Cretaceous abundance is equal to the Bathonian peak. Abundance remains relatively consistent until the Aptian, which is comparable to the Kimmeridgian-Tithonian, and reaches its zenith in the Albian (Fig. 7.1). Abundance in the Late Cretaceous is similar to pre-Bathonian levels.

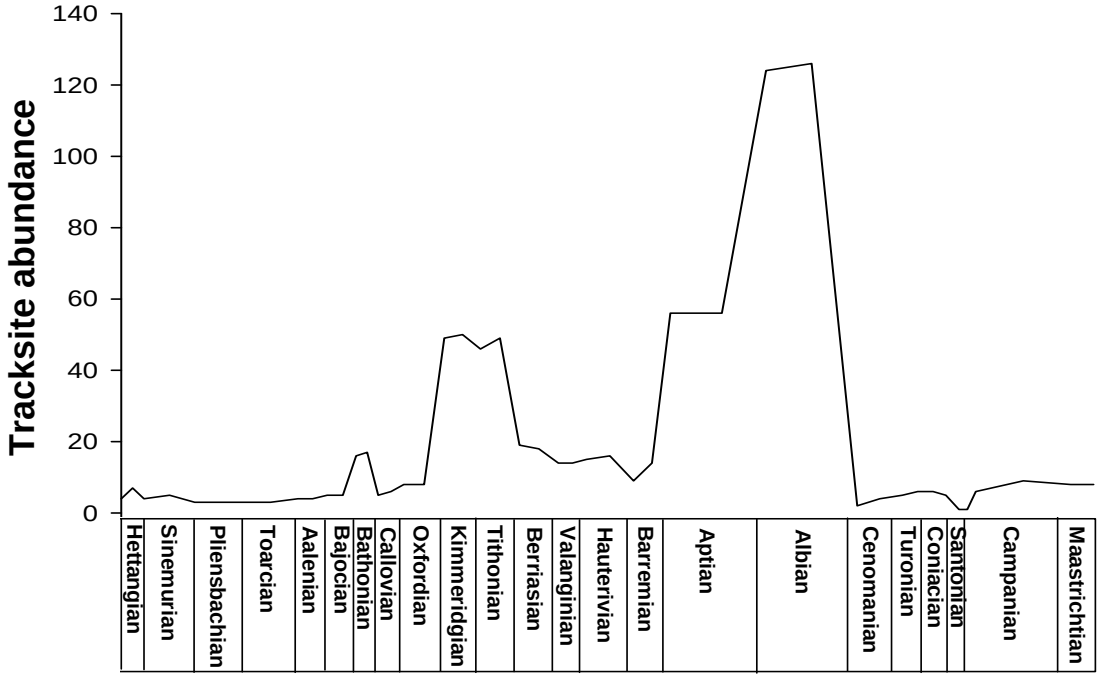

FIGURE 7.1. Sauropod tracksite abundance through time.

A similar pattern is observed when tracksite region abundance is considered (see Table 7.1 for a statistical comparison), although there are a few slight differences (Fig. 7.2). A Bathonian peak is still present but abundance increases more gradually up to this time period. A peak in abundance can also still be observed in the Kimmeridgian-Tithonian,

although this is now the apogee of abundance, rather than the Aptian-Albian. Lastly, a peak is also now present in the Maastrichtian.

Comparisons	Spearman's rs	Kendall's tau
Sauropod tracksites vs. regions	0.796 (p<0.001)	0.636 (p<0.001)
Sauropods vs. Ornithischians	0.398 (p=0.007)	0.278 (p=0.014)
Sauropods vs. Ornithischians (J)	0.362 (p=0.089)	0.285 (p=0.083)
Sauropods vs. Ornithischians (K)	0.465 (p=0.027)	0.341 (p=0.027)
Sauropods vs. Ornithischians (EK)	0.846 (p=0.004)	0.730 (p=0.003)
Sauropods vs. Ornithischians (LK)	0.118 (p=0.730)	0.083 (p=0.778)
Sauropods vs. TDE	0.340 (p=0.024)	0.251 (p=0.023)
Sauropods vs. TDE (J)	0.536 (p=0.016)	0.404 (p=0.018)
Sauropods vs. TDE (K)	0.088 (p=0.704)	0.088 (p=0.593)
Sauropods vs. TDE (EK)	0.586 (p=0.056)	0.443 (p=0.067)
Sauropods vs. TDE (LK)	0.873 (p=0.001)	0.767 (p=0.001)

TABLE 7.1. Results of statistical analyses comparing sauropod tracksite abundance with ornithischian tracksite abundance and sauropod taxic diversity. J=Jurassic; K=Cretaceous; EK=Early Cretaceous; LK=Late Cretaceous; TDE=sauropod taxic diversity; Sauropods=sauropod tracksite abundance; Ornithischians=ornithischian tracksite abundance.

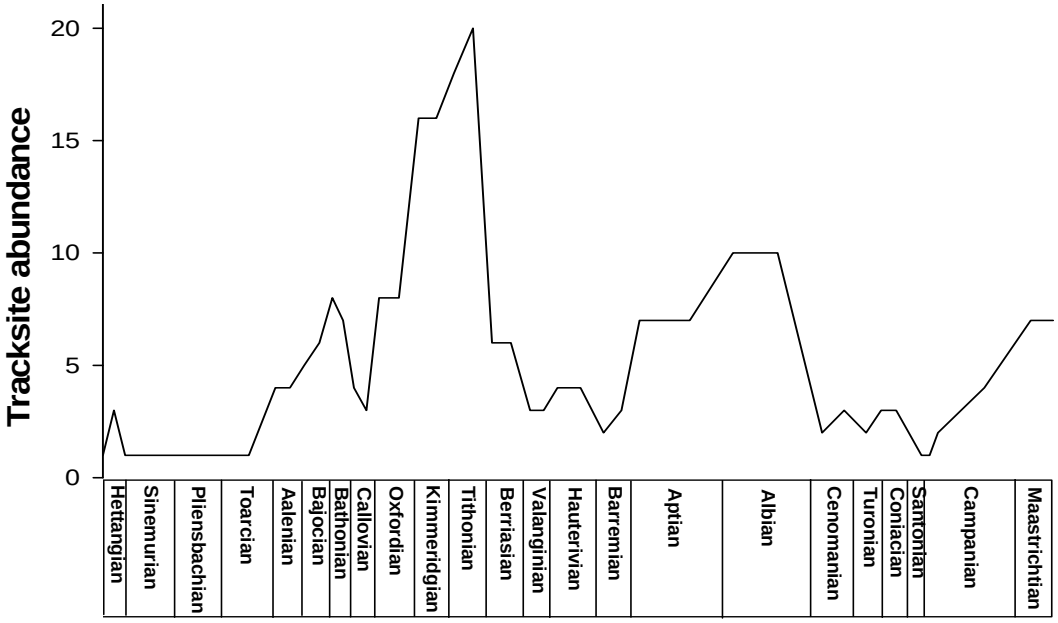

FIGURE 7.2. Sauropod tracksite region abundance (based on geographical region [e.g. state], following Farlow [1992], so that only one tracksite is represented per region for each time bin) through time.

Comparison with ornithischian tracksite abundance

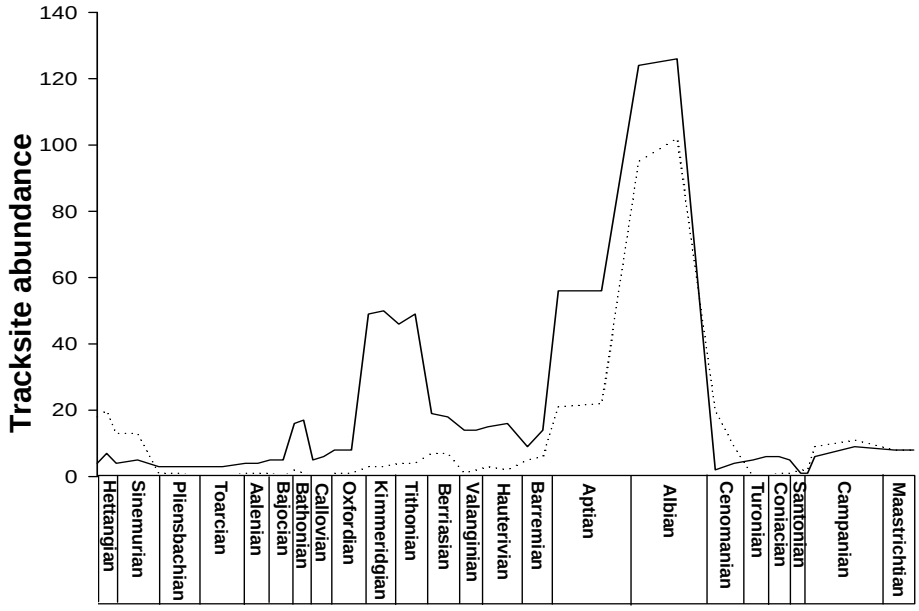

FIGURE 7.3. Sauropod (solid line) and ornithischian (dotted line) tracksite abundance through time.

There is a positive, though relatively weak, correlation when sauropod and ornithischian tracksite abundance are compared with one another (Fig. 7.3) throughout the Jurassic-Cretaceous (Table 7.1). This weak correlation also remains when the Jurassic and Cretaceous are considered separately (see Table 7.1). A much stronger correlation is recovered when the Early Cretaceous is considered by itself; however, there is no correlation between the two tracksite abundances for the Late Cretaceous (Table 7.1).

Comparison with sauropod diversity

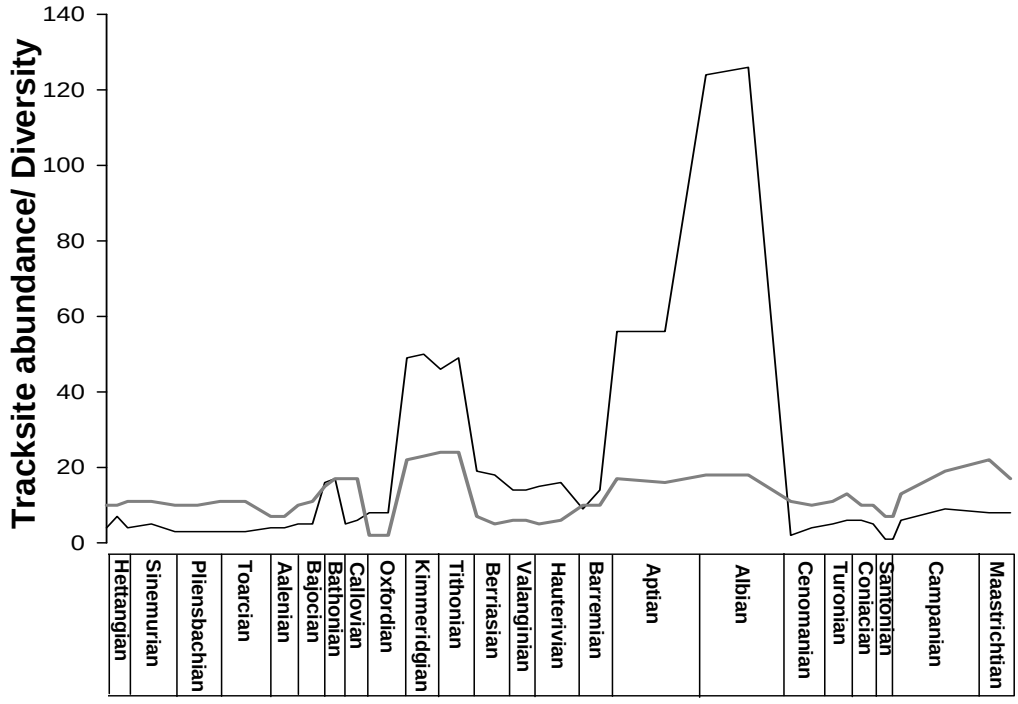

FIGURE 7.4. Sauropod tracksite abundance (black line) and sauropod diversity (grey line) through time.

Comparison between sauropod tracksite abundance and taxic diversity (TDE) reveals a weak positive correlation for the Jurassic-Cretaceous (Table 7.1; Fig. 7.4). This correlation is strengthened when only the Jurassic is considered, but disappears for the Cretaceous. However, the correlation is present for the Early Cretaceous and becomes

very strongly supported when only the Late Cretaceous is considered (Table 7.1). This discrepancy suggests that long term trends are being obscured (perhaps by stratigraphical error or lagerstätten effects), whereas these problems are ameliorated in analyses of smaller time trends.

Comparison with the rock record

A positive correlation exists between sauropod tracksite abundance and both DBFs (Fig. 7.5) and DBCs (Fig. 7.6; Table 7.2). This correlation is more strongly supported when the Jurassic is considered on its own, but is also present for the Cretaceous Period. The Early Cretaceous displays similar levels of correlation, while there is no correlation for the Late Cretaceous (Table 7.2).

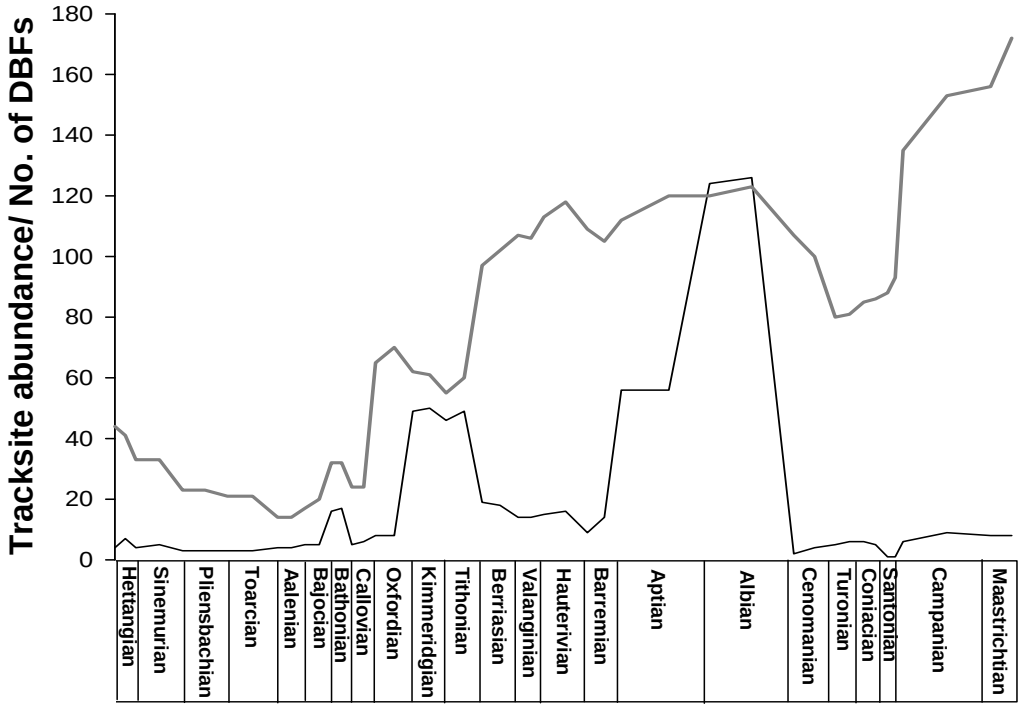

FIGURE 7.5. Sauropod tracksite abundance (black line) and numbers of dinosaur-bearing formations (grey line) through time.

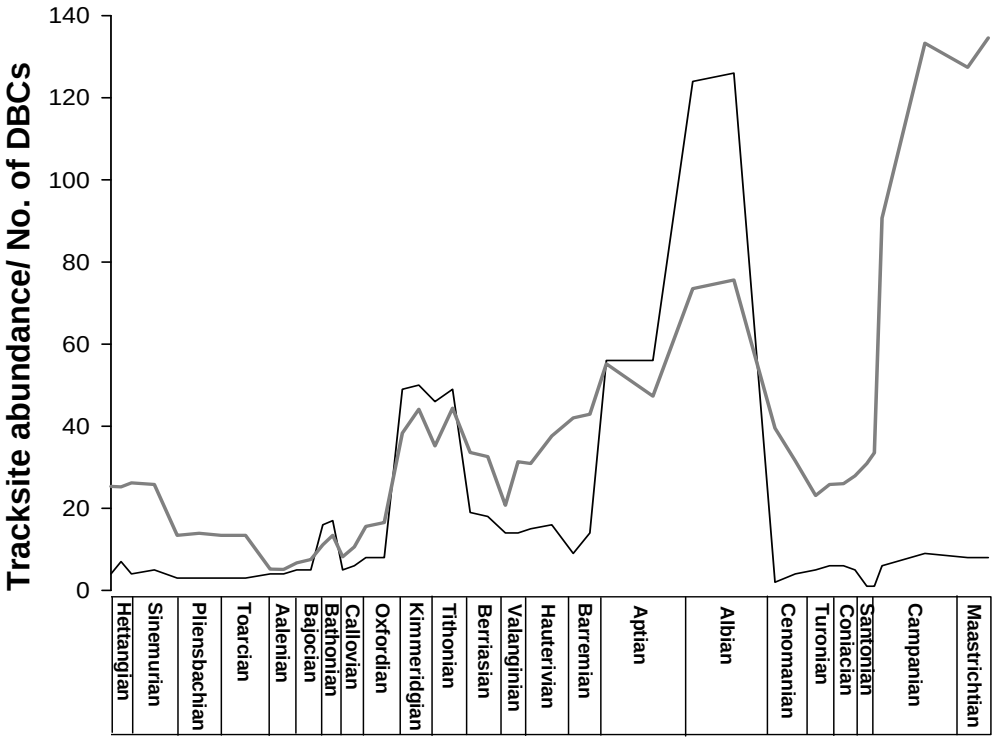

FIGURE 7.6. Sauropod tracksite abundance (black line) and numbers of dinosaur-bearing collections (grey line) through time. Note that DBCs have been divided by 10 to allow the two curves to be plotted together.

Comparisons	Tracksites		Tracksite regions	
	Spearman's rs	**Kendall's tau**	**Spearman's rs**	**Kendall's tau**
DBFs	0.466 (p=0.001)	0.323 (p=0.001)	0.191 (p=0.188)	0.141 (p=0.178)
DBFs (J)	0.690 (p=0.002)	0.514 (p=0.003)	0.484 (p=0.025)	0.319 (p=0.052)
DBFs (K)	0.464 (p=0.014)	0.301 (p=0.033)	0.599 (p=0.004)	0.442 (p=0.004)
DBFs (EK)	0.542 (p=0.063)	0.394 (p=0.085)	0.540 (p=0.081)	0.388 (p=0.105)
DBFs (LK)	0.443 (p=0.153)	0.286 (p=0.243)	0.497 (p=0.119)	0.382 (p=0.134)
DBCs	0.519 (p<0.001)	0.377 (p<0.001)	0.284 (p=0.049)	0.198 (p=0.062)
DBCs (J)	0.477 (p=0.027)	0.376 (p=0.018)	0.255 (p=0.260)	0.174 (p=0.297)
DBCs (K)	0.343 (p=0.087)	0.244 (p=0.097)	0.522 (p=0.010)	0.390 (p=0.011)
DBCs (EK)	0.674 (p=0.018)	0.563 (p=0.013)	0.656 (p=0.021)	0.529 (p=0.020)
DBCs (LK)	0.435 (p=0.157)	0.286 (p=0.235)	0.439 (p=0.160)	0.316 (p=0.201)

Terrestrial rock	0.574 (p<0.001)	0.375 (p<0.001)	0.336 (p=0.021)	0.241 (p=0.022)
Terrestrial rock (J)	0.526 (p=0.014)	0.370 (p=0.023)	0.488 (p=0.022)	0.359 (p=0.025)
Terrestrial rock (K)	0.590 (p=0.002)	0.389 (p=0.006)	0.349 (p=0.093)	0.207 (p=0.186)
Terrestrial rock (EK)	-0.670 (p=0.024)	-0.426 (p=0.072)	-0.674 (p=0.023)	-0.437 (p=0.067)
Terrestrial rock (LK)	0.379 (p=0.209)	0.167 (p=0.507)	0.356 (p=0.270)	0.261 (p=0.314)
Marine rock	-0.543 (p<0.001)	-0.349 (p<0.001)	-0.323 (p=0.031)	-0.225 (p=0.041)
Marine rock (J)	-0.312 (p=0.154)	-0.227 (p=0.161)	-0.262 (p=0.241)	-0.232 (p=0.171)
Marine rock (K)	-0.545 (p=0.008)	-0.344 (p=0.024)	-0.493 (p=0.017)	-0.350 (p=0.023)
Marine rock (EK)	0.513 (p=0.091)	0.361 (p=0.127)	0.516 (p=0.092)	0.370 (p=0.121)
Marine rock (LK)	-0.565 (p=0.056)	-0.433 (p=0.068)	-0.356 (p=0.248)	-0.261 (p=0.289)
SCM1	-0.294 (p=0.054)	-0.208 (p=0.055)	-0.120 (p=0.424)	-0.057 (p=0.614)
SCM2	-0.094 (p=0.554)	-0.054 (p=0.644)	0.016 (p=0.915)	0.022 (p=0.832)
CCM1	-0.228 (p=0.131)	-0.135 (p=0.212)	-0.111 (p=0.471)	-0.038 (p=0.722)
CCM2	-0.096 (p=0.498)	-0.053 (p=0.605)	-0.033 (p=0.821)	-0.004 (p=0.979)
SCM1 (EK)	-0.647 (p=0.023)	-0.441 (p=0.045)	-0.654 (p=0.025)	-0.436 (p=0.065)
CCM1 (EK)	-0.576 (p=0.052)	-0.378 (p=0.091)	-0.590 (p=0.036)	-0.371 (p=0.090)
Sea level	0.125 (p=0.393)	0.115 (p=0.270)	0.113 (p=0.437)	0.086 (p=0.417)
Sea level (J)	0.584 (p=0.005)	0.457 (p=0.005)	0.809 (p<0.001)	0.657 (p<0.001)
Sea level (K)	-0.709 (p<0.001)	-0.455 (p=0.001)	-0.459 (p=0.021)	-0.269 (p=0.081)
Sea level (EK)	0.459 (p=0.142)	0.438 (p=0.065)	0.454 (p=0.141)	0.433 (p=0.081)
Sea level (LK)	-0.343 (p=0.275)	-0.191 (p=0.446)	-0.482 (p=0.104)	-0.349 (p=0.156)

TABLE 7.2. Results of statistical analyses comparing sauropod tracksite and tracksite region abundance with sampling proxies. J=Jurassic; K=Cretaceous; EK=Early Cretaceous; LK=Late Cretaceous; DBFs=dinosaur-bearing formations; DBCs=dinosaur-bearing collections; SCM=skeletal completeness metric; CCM=character completeness metric.

Comparisons between sauropod tracksite abundance and the western European rock outcrop area dataset of Smith and McGowan (2007) show a positive correlation with

terrestrial rock outcrop and a negative correlation with marine rock outcrop area for the Jurassic-Cretaceous (Table 7.2; Fig. 7.7). Similar correlations are recovered when the Jurassic and Cretaceous are considered separately (Table 7.2). The marine rock record displays a positive correlation with abundance in the Early Cretaceous, while there a negative correlation between abundance and terrestrial rock for this same epoch. There is also a negative correlation between marine rock and abundance in the Late Cretaceous, but no statistically meaningful relationship when the terrestrial rock record is compared (Table 7.2). When the tracksite data is restricted to European occurrences, the same correlations are found for the Late Jurassic-Cretaceous and for the Jurassic by itself; however, there are no statistically significant correlations in the Cretaceous (Table 7.3).

Comparisons	**Tracksites**	
	Spearman's rs	**Kendall's tau**
Terrestrial rock	0.451 (*p*=0.001)	0.339 (*p*=0.003)
Terrestrial rock (J)	0.664 (*p*=0.003)	0.555 (*p*=0.001)
Terrestrial rock (K)	0.379 (*p*=0.095)	0.280 (*p*=0.109)
Terrestrial rock (EK)	-0.251 (*p*=0.440)	-0.168 (*p*=0.507)
Terrestrial rock (LK)	0.024 (*p*=0.966)	0.041 (*p*=0.947)
Marine rock	-0.369 (*p*=0.014)	-0.256 (*p*=0.019)
Marine rock (J)	-0.463 (*p*=0.027)	-0.413 (*p*=0.011)
Marine rock (K)	-0.300 (*p*=0.144)	-0.196 (*p*=0.224)
Marine rock (EK)	0.287 (*p*=0.376)	0.235 (*p*=0.350)
Marine rock (LK)	0.056 (*p*=0.896)	0.041 (*p*=0.932)

TABLE 7.3. Results of statistical analyses comparing European sauropod tracksite abundance with western European rock outcrop.

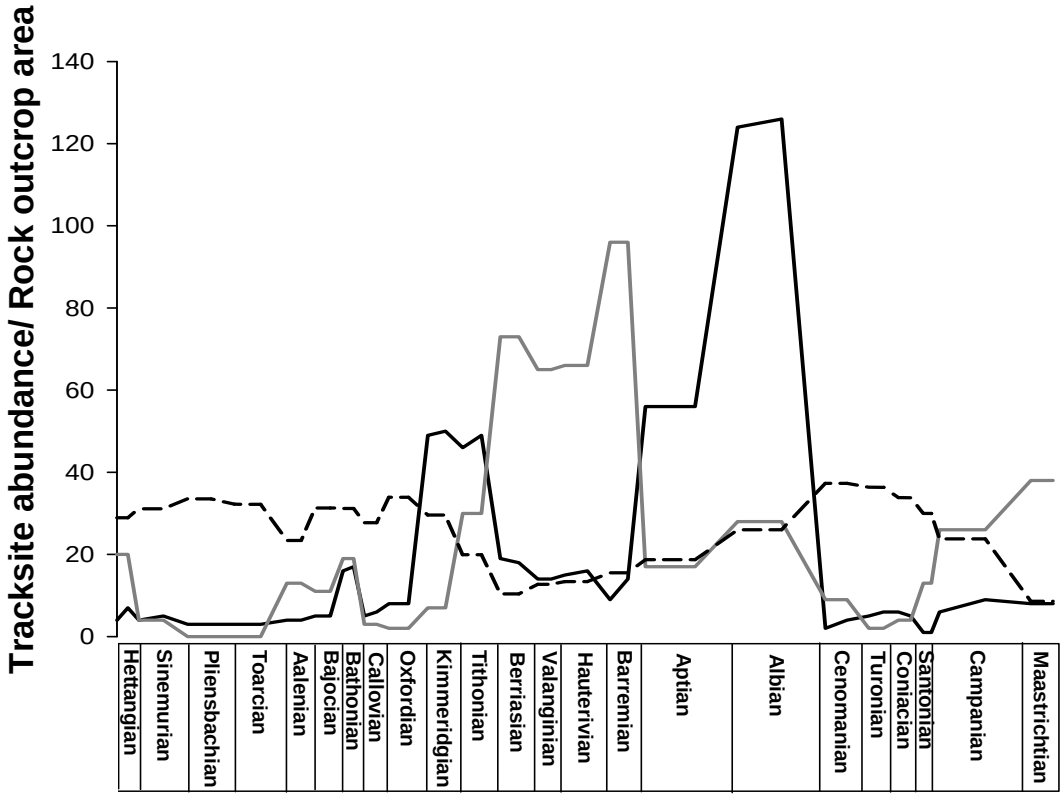

FIGURE 7.7. Sauropod tracksite abundance (black line) and western European rock outcrop area (terrestrial [grey line] and marine [dashed line]) through time. Note that marine rock outcrop values have been divided by 10 to allow the three curves to be plotted together.

Comparison with specimen completeness

Although all four completeness metrics (SCM1-2 and CCM1-2) have been demonstrated to be strongly correlated with one another ($p < 0.001$; see Chapter 5), only SCM1 shows any statistically significant correlation with tracksite abundance (Fig. 7.8), and this correlation is extremely weak (Table 7.2). When the tracksite data are partitioned into smaller time bins there is no evidence for a correlation in the Jurassic ($p > 0.3$ for all tests), Cretaceous ($p > 0.2$ for all tests) or Late Cretaceous ($p > 0.7$ for all tests). Consideration of the Early Cretaceous by itself, however, reveals a relatively strong

negative correlation (Table 7.2) between abundance and SCM1 (and to a lesser extent CCM1; SMC2 and CCM2 still show no statistically significant correlation), indicating that tracksite abundance increases at times when specimen completeness is low. However, this negative correlation in the Early Cretaceous is a result of a peak in tracksite abundance in the Aptian-Albian, coinciding with a trough in specimen completeness: re-running the analyses after excluding these two stages results in no correlation for the Early Cretaceous ($p > 0.9$ for all tests).

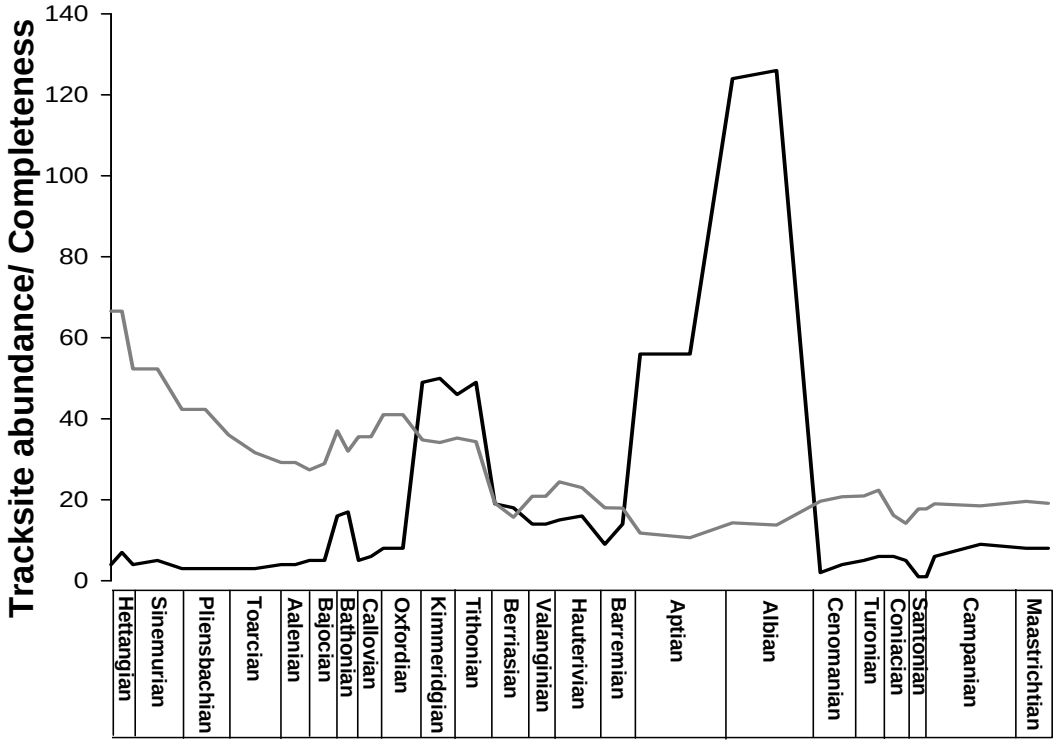

FIGURE 7.8. Sauropod tracksite abundance (black line) and Skeletal Completeness Metric 1 [SCM1] (grey line) through time.

Comparison with sea level

There is no correlation between sauropod tracksite abundance and the sea level curve of Haq *et al*. (1987) (Table 7.2) for the Mesozoic (Fig. 7.9). A positive correlation is recovered when the Jurassic is considered by itself and a notably strong negative

correlation is present for the Cretaceous. There is no correlation when the Early and Late Cretaceous are investigated separately (Table 7.2).

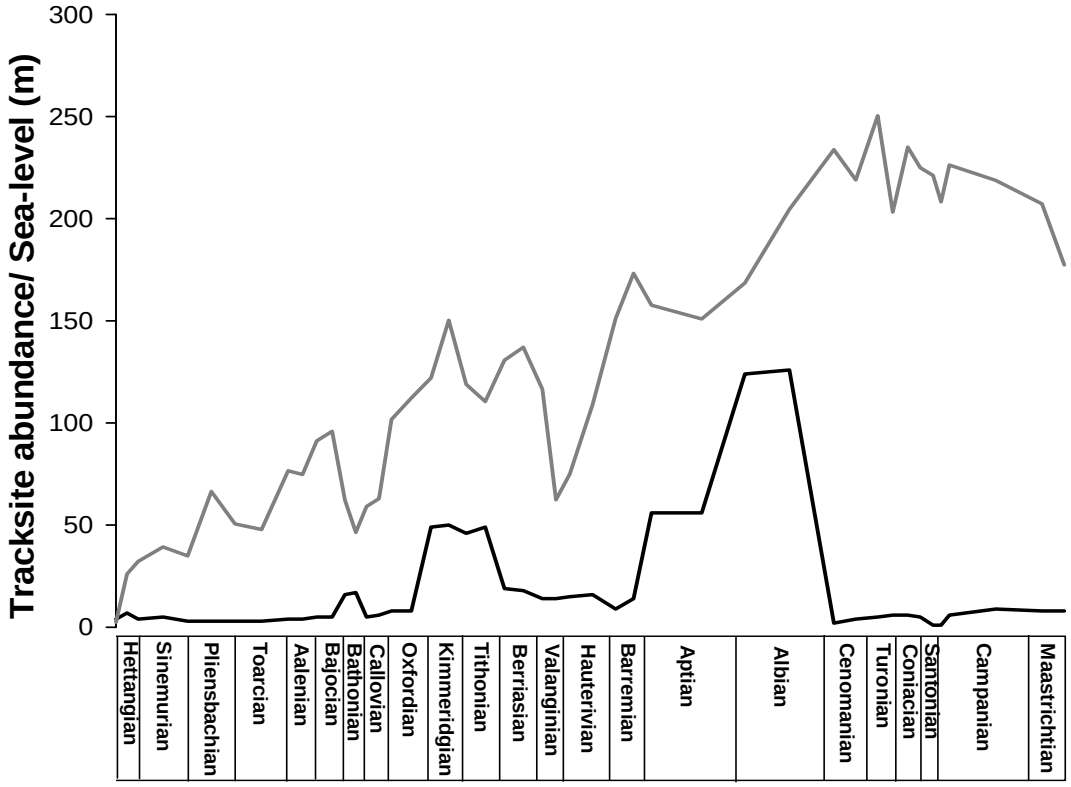

FIGURE 7.9. Sauropod tracksite abundance (black line) and the sea-level curve of Haq *et al*. (1987 [grey line]) through time.

Discussion

As noted in Chapter 6, the two herbivorous dinosaurian clades began to occupy different palaeolatitudes in the Cretaceous, with this difference particularly marked in the Late Cretaceous. It is possible that this palaeolatitudinal skew may explain the differences in tracksite abundance between the two groups during this epoch. Whether this skew is a result of differing preservational potentials for the two latitudinal zones, or reflects a genuine disparity in the abundance of each group, remains to be seen; however, it is difficult to explain why sauropods and ornithischians would be affected by different taphonomic biases in each palaeolatitudinal zone.

The overall correlation between sauropod tracksite abundance and diversity is perhaps unsurprising. Counts of both abundance and diversity can be affected by taphonomic processes (see Butler *et al*. 2009): during well-sampled time periods one would expect to preserve a greater number of individuals, as well as a larger representation of genus richness, than at times of poor sampling.

Rock outcrop appears to exert a strong influence on tracksite numbers in the Jurassic, implying that abundance is controlled by the number of opportunities to observe (NOOs) in this period. The Early Cretaceous is more difficult to understand: NOOs do seem to exert an influence on abundance; however, in contrast, western European terrestrial rock is negatively correlated with abundance. This may be explained by the lack of European tracksites from this time period (just 11% of this subset of the data): if western European is not a suitable proxy for global rock outcrop (as has been suggested in both Chapters 4 and 5) then there is no reason to expect a correlation here. In fact, when non-European tracksites are excluded from the analyses, there is no correlation in the Cretaceous. However, it may be that the amount of rock area is not the full driver of tracksite abundance; instead, fluctuations in the type of rock and depositional environments preserved may have a greater impact on the potential for trackways to be

preserved, but a lack of refined data means this cannot be currently investigated. Abundance in the Late Cretaceous appears to be largely removed from the effects of NOOs or rock outcrop area.

Both sea level and abundance reach their Jurassic peak in the Kimmeridgian-Tithonian. However, none of the other peaks or troughs in this time period appears to correlate: for example, sea level is higher in the Bajocian than in the Bathonian. Nevertheless, the overall fluctuations in abundance in this period do seem to be partly controlled by sea level. It is possible that this reflects the positive association between non-titanosaurs (the majority of sauropods) and coastal environments. In general, Cretaceous sea levels are much higher than in Jurassic times and there is a negative correlation between sea level and abundance for this time interval. However, when the Cretaceous is separated into epochs, this correlation disappears. It seems likely that this Cretaceous correlation results from mid-Cretaceous fluctuations: abundance is high in the Albian while tracksite occurrences are extremely rare in the Cenomanian, a time period which conversely has higher sea levels. The lack of a correlation in the Cretaceous may reflect the inland association of most sauropods (i.e. titanosaurs).

CHAPTER EIGHT

TAPHONOMY

Analyses and Results

The full dataset has been analysed, with clades and grades of sauropodomorphs (non-sauropod sauropodomorphs, non-neosauropod sauropodomorphs, neosauropods, diplodocoids, macronarians, titanosauriforms and titanosaurs) also examined to investigate whether taphonomic processes affect them in different ways. The dataset has then been refined in different ways for four separate analyses:

1. Analyses have been implemented for all individuals at least 10% and 20% complete. Completeness of specimens has been determined using SCM1. This metric attempts to capture a combination of the number of elements preserved as well as their physical bulk, and is potentially more useful than the 'Character Completeness Metric' (CCM: see Chapter 5) in taphonomic studies.

2. Analyses including only those individuals that are at least partly articulated (i.e. at least two elements of the skeleton in articulation) have been run, while disarticulated and isolated remains have been excluded. These have been omitted so that the remaining specimens are restricted to those that are unlikely to have been transported a significant distance from their place of death.

3. Individuals have been divided into their environment of deposition, using the broad categories of inland and coastal (see Chapter 2 and 3). Again, the limitations and crudeness of this division are acknowledged (see Chapter 2).

4. An analysis has also been implemented to attempt to determine the disarticulation sequence of sauropodomorphs. Sauropodomorph specimens have been grouped into taphonomic bins, using the SCM1, with the elements lost at each 'stage' of decreasing completeness mapped out to highlight the order of disarticulation. The dataset for this analysis has been restricted to only those individuals that are both =>20% complete and

display some degree of articulation. The exclusion of disarticulated remains increases the likelihood of skeletons only representing a single individual; furthermore, the inclusion of entirely disarticulated individuals makes it impossible to determine the order of disarticulation.

Total evidence

Region	A (1203)	B (182)	C (459)	D (744)	E (216)	F (520)	G (395)	H (257)
Skull	197	59	101	96	27	69	35	25
Teeth	125	3	41	84	11	69	50	16
Cervicals	264	60	129	135	47	87	65	37
Pectoral	261	61	125	136	42	94	69	44
Forelimbs	399	76	184	215	68	144	115	72
Dorsals	369	84	173	196	60	133	96	65
Pelvic	369	92	180	189	65	123	91	60
Sacrum	211	63	111	100	36	62	45	32
Hindlimbs	532	131	251	281	94	183	147	99
Caudals	503	74	192	311	81	229	189	146
Osteoderms	18	N/A	N/A	18	N/A	18	18	18

TABLE 8.1. Preserved body regions of sauropodomorph individuals. A=all sauropodomorphs; B=non-sauropod sauropodomorphs; C=non-neosauropod sauropodomorphs; D=neosauropods; E=diplodocoids; F=macronarians; G=titanosauriforms; H=titanosaurs. Numbers in brackets represent the number of individuals of that given subset of sauropodomorphs.

Elements of the hindlimbs and tail are the regions most commonly preserved (see Table 8.1). Hindlimbs are preserved in abundance in basal sauropodomorphs (B + C), while the same is true for caudal vertebrae in titanosaurs (H). Half of all basal sauropodomorphs

(B) preserve pelvic material, while this region of the body is only preserved in 25% of neosauropods (D). Similarly, basal forms (B + C) tend to be more likely to preserve elements of the cervical and dorsal vertebrae, sacrum, pectoral girdle and forelimbs (Table 8.1). Within neosauropods, there is much less variation, although diplodocoids (E) tend to consistently preserve greater amounts of the body than Macronaria (F) and its constituent clades (although these differences are not statistically significant). Regarding the skull, 32% of basal sauropodomorphs (B) preserve cranial material; this is in comparison to 22% to non-neosauropod sauropodomorphs (C) and just 13% in neosauropods (D). Within Neosauropoda, diplodocoids and macronarians tend to preserve skulls as often as one another. Conversely, teeth recovered without cranial material are exceedingly rare in basal sauropodomorphs (B), a little more common in diplodocoids (5%) and an order of magnitude more common in macronarians and titanosauriforms (13%), although titanosaurs (6%) preserve a similar amount as diplodocoids (Table 8.1).

Degree of completeness

Elements of the dorsal vertebrae, hindlimbs and pelvic girdle tend to be the most commonly preserved regions when the dataset is restricted to >=10% and >=20% complete individuals (Table 8.2). The percentage of individuals preserving skull material is consistently around 30-37% for basal forms and diplodocoids, although cranial material is recovered more often in the former than in neosauropods. Only 16-17% of titanosaur individuals preserve cranial remains. As also noted in the 'total evidence' dataset, caudal vertebrae are the most commonly preserved elements in titanosaurs and are much more common than in diplodocoids. The other notable difference observed when individual clades are investigated is the high percentage of diplodocoid individuals that preserve cervical vertebrae (Table 8.2).

Region	Sauropodomorphs (322/184)	Non-neosauropods (168/135)	Neosauropods (154/75)	Diplodocoids (53/30)	Titanosaurs (51/18)
Skull	98/69	60/48	38/21	17/10	8/3
Teeth	12/6	7/4	5/2	1/0	2/1
Cervicals	187/135	99/79	88/56	38/26	24/13
Pectoral	186/120	99/73	87/47	27/17	28/10
Forelimbs	200/124	112/75	88/49	26/18	33/14
Dorsals	243/167	128/97	115/70	40/29	38/16
Pelvic	235/155	127/92	108/63	38/26	35/14
Sacrum	165125	91/72	74/53	29/22	22/12
Hindlimbs	249/159	139/96	110/63	36/26	39/14
Caudals	224/145	111/81	113/64	34/23	45/17
Osteoderms	4/3	N/A	4/3	N/A	4/3

TABLE 8.2. Preserved body regions of sauropodomorph individuals which are >=10% and 20% complete (using the SCM1). In each case the first value is >=10% and the second >=20%.

Articulated specimens

When considering all sauropodomorph individuals, the percentages of body regions are preserved in the following decreasing order: hindlimbs, caudals, dorsals, pelvis, cervicals, forelimbs, sacrum, pectoral girdle and skull (Table 8.3). Isolated teeth and osteoderms are the most rarely preserved. This overall pattern remains when individual clades are considered, with only minor changes. For example, caudal vertebrae are the most commonly preserved elements for all sauropods, while cervicals are the third most common body region to be preserved in diplodocoids but seventh in macronarians. Similarly, hindlimb and forelimb material are the fifth and eight, respectively, most

commonly preserved regions in diplodocoids, while in macronarians they are the second and fifth (although there is no statistical significance in the differences between the two clades). The percentage of individuals with skulls also varies, with 33% of diplodocoids preserving cranial material compared to just 14% in titanosaurs, which is comparable to the values observed in the 'completeness' data subsets. There are similarly large differences between these two clades in the pectoral and cervical regions (Table 8.3).

Region	A (334)	B (106)	C (170)	D (164)	E (51)	F (112)	G (78)	H (51)
Skull	99	41	58	41	17	24	13	7
Teeth	11	1	6	5	1	4	3	3
Cervicals	149	45	79	70	30	40	27	17
Pectoral	119	39	67	52	20	32	19	10
Forelimbs	145	46	83	62	18	43	30	20
Dorsals	190	67	102	88	31	56	42	28
Pelvic	175	62	95	80	27	52	36	22
Sacrum	138	49	74	64	22	41	28	20
Hindlimbs	204	81	119	85	26	58	43	26
Caudals	195	53	93	102	33	68	51	38
Osteoderms	4	N/A	N/A	4	N/A	4	4	4

TABLE 8.3. Preserved body regions of sauropodomorph individuals which were found in articulation. See Table 8.1 for abbreviations.

Taphonomy across environments

Although hindlimbs are still recovered as one of the most commonly preserved body regions in both inland and coastal environments, caudal vertebrae are only common in inland settings: in coastal environments only 26% of individuals preserve tail elements (Table 8.4). Forelimb material and isolated teeth are much more common in coastal

than inland settings, while skull, cervical, dorsal and sacral remains are better represented in inland environments. Other body regions (i.e. the pectoral and pelvic girdles) are found equally often in both environments.

Region	A (I=997, C=140)	B (I=171, C=2)	C (I=399, C=30)	D (I=598, C=110)	E (I=164, C=40)	F (I=429, C=65)	G (I=312, C=59)	H (I=234, C=11)
Skull	181/11	57/0	98/1	83/10	23/4	60/6	26/6	23/0
Teeth	91/27	3/0	30/8	61/19	7/2	51/16	38/11	16/0
Cervicals	235/21	57/1	121/5	114/16	39/8	74/8	52/8	35/1
Pectoral	224/26	57/2	115/6	109/20	31/9	78/11	53/11	41/1
Forelimbs	326/63	72/2	163/16	163/47	45/23	115/24	86/24	65/5
Dorsals	327/27	80/0	163/4	164/23	47/11	115/12	78/12	61/2
Pelvic	323/36	89/2	167/9	156/27	51/14	104/13	72/13	57/3
Sacrum	193/10	60/2	106/2	87/8	33/3	53/5	36/5	29/3
Hindlimbs	455/61	123/2	225/13	230/48	73/21	154/27	118/27	94/5
Caudals	433/37	70/1	171/11	262/26	66/10	195/16	157/15	132/5
Osteoderms	18/0	N/A	N/A	18/0	N/A	18/0	18/0	18/0

TABLE 8.4. Preserved body regions of sauropodomorph individuals for different environments for various groups. In each case the first value is the inland total and the second is the coastal total. See Table 8.1 for abbreviations.

When individual clades are considered, some additional patterns emerge (Table 8.4). For example, there is no statistically meaningful difference between the number of neosauropod skulls found in inland and coastal environments. However, although not statistically significant, of note is that no titanosaur skull materials are known from coastal settings, nor are there any isolated teeth or osteoderms from such environments (Table 8.4). Neosauropod sacral materials remain much more commonly

found in inland environments; however, when the various neosauropod clades are analysed separately, there is no evidence for a bias towards either environment. None of the titanosaur analyses produce statistically significant results. The results from non-sauropod sauropodomorphs are ignored as just two coastal individuals are known (Table 8.4).

Disarticulation sequence

Completeness class	Disarticulation sequence – loss of elements
80%+	Phalanges, manual elements, chevrons
70-79%	Posterior half of tail, sternal plates, lower forelimbs and hindlimbs, skull elements
60-69%	Anterior portion of neck, posterior ¾ of the tail, more skull elements
50-59%	Pectoral girdle elements, anterior half of the neck, most of the skull
40-49%	Skull, neck, forelimbs, anterior portion of the dorsals, pectoral girdle, pelvic and sacral elements
30-39%	Anterior half of dorsals, hindlimb elements, sacrum, most of the pelvis, most of the tail
20-29%	Most of the dorsals, most of the hindlimbs

TABLE 8.5. Sauropodomorph disarticulation sequence. Completeness classes refer to the Skeletal Completeness Metric (SCM).

Table 8.5 displays the disarticulation sequence of sauropodomorphs. The first elements to be lost tend to be extremities and unfused bones, e.g. chevrons, phalanges and manual and pedal elements in general. The posterior half of the tail also tends to disarticulate early on, along with the sternal plates and elements of the lower forelimbs and lower hindlimbs. The skull tends to be next to be lost (with the palate often first to disarticulate), followed by the anterior region of the neck and the posterior three-

quarters of the tail. These regions become increasingly disarticulated, along with elements of the pectoral girdle. Complete loss of the skull and neck follows, along with loss of forelimbs and the remainder of the pectoral girdle. The anterior dorsals then begin to disarticulate, along with hindlimb, sacral and pelvic elements. These regions, along with the proximal part of the tail then gradually become increasingly disarticulated.

Discussion

The sauropodomorph disarticulation sequence is largely as expected, with extremities the first to be lost, followed by a gradual loss of elements from the front, back and lower parts (i.e. lower limbs) of the body.

It seems clear that basal forms tend to preserve more complete skeletons than more derived sauropods. Although testing of this idea is beyond the scope of this study, it is possible that this relates to differences in body size. Most basal sauropodomorphs tend to be relatively small animals (see Galton and Upchurch 2004; Barrett and Upchurch 2007), while derived forms include the largest known terrestrial animals. Although it is possible that large animals may stand a greater chance of being preserved in the fossil record (Behrensmeyer *et al*. 1979), their large size makes it extremely unlikely that the whole animal will be preserved, given the larger amount of sediment needed for rapid burial. This may explain why so many derived sauropods are known from isolated bones, while many 'prosauropods' and other basal forms are known from relatively complete animals.

Although many of the differences in percentages appear to be genuine, it is likely that some merely reflect our ability to recognise particular clades. For example, prominent procoely in the tail is diagnostic of Titanosauria and this may explain why this clade is known from caudal vertebrae more than any other clade. However, it seems unlikely that this can explain differences in the preservation of cranial material. One possibility is that because derived sauropod skulls are much more open than basal forms, they are potentially more susceptible to destructive taphonomic processes. However, this does not explain why articulated and relatively complete diplodocoid individuals preserve cranial material more often than titanosaurs; this may relate to more fine-scale differences in depositional environment that are not captured in the current analyses.

Although none of the results of environmental analyses pertaining to titanosaurs are statistically significant, one interesting aspect worth noting is the lack of osteoderms recovered in coastal environments. These structures are only known in derived titanosaurs (i.e. lithostrotians) and it has been argued that these animals demonstrated a preference for inland environments (see Chapter 3). It is therefore interesting to note that not a single one is known from a coastal setting, despite their potential susceptibility to transportation, suggesting that these animals were perhaps living fully inland.

CHAPTER NINE

CONCLUSIONS AND FUTURE WORK

Conclusions

1. The results of the analyses of environmental associations suggest that titanosaurs and non-titanosaurs display statistically significant positive associations with inland and coastal settings respectively. These signals occur when body fossils and trackway data are treated separately and together, for both locality-based and individual-based counts of occurrences. This pattern is interpreted to mean that sauropod groups displayed habitat preferences, although the precise nature and strength of this preference is not clear at present. Wilson and Carrano's (1999) hypothesis that wide-gauge trackways were made by titanosaurs is reinforced by the observation that separate analyses of titanosaur body fossils and wide-gauge trackways display the same positive association with inland habitats. Such an association, alongside several other lines of evidence, supports the view that the absence of sauropods in the early Late Cretaceous of Europe and North America is most plausibly interpreted as a sampling bias related to the dominance of coastal sediments preserved in these regions. Finally, although the decline of non-titanosaurs and diversification of titanosaurs during the Early and early Late Cretaceous cannot be linked directly to habitat preferences, an understanding of such preferences may contribute to the explanation of these events in future studies.

Ecologists and invertebrate palaeontologists have been investigating environmental associations for several decades; however, the search for statistically robust associations among fossil vertebrate taxa is in its infancy. It is crucial that palaeobiologists test their ecological and evolutionary hypotheses using analytical methods and statistical tests that are capable of distinguishing genuine signals from the background noise generated by missing data and sampling biases. At the same time, it is also vital that these techniques be applied, and their results interpreted, with subtlety and caution. The current study has demonstrated that both 'total evidence' and time-slicing approaches have their costs and benefits, and that parallel trends in diversity and the representation of environments can create skews in spatial distributions that result

in statistically significant but nonetheless artefactual support for environmental associations.

2. Through comparison of a number of different sampling proxies and use of several methods, there are certain time periods for which sauropodomorph diversity seems to reflect genuine biological effects rather than the vagaries of the fossil record. Peaks are consistently recovered for the Pliensbachian–Toarcian, Bathonian–Callovian and Kimmeridgian–Tithonian, suggesting that these represent time intervals of genuinely high sauropodomorph diversity, as also indicated by previous authors (e.g. Hunt *et al*. 1994; Barrett and Willis 2001; Upchurch and Barrett 2005; Barrett *et al*. 2009). The Oxfordian is repeatedly shown to represent a depauperate fauna, despite an apparently good rock record at this time, which is consistent with the study of Upchurch and Barrett (2005), although issues remain regarding the poor dating of some fossil-bearing localities. Similarly, the J/K boundary appears to represent a real crash in sauropod diversity, supporting the findings of previous authors (e.g. Hunt *et al*. 1994; Upchurch and Barrett 2005; Barrett *et al*. 2009), and may be related to the South African Morokweng impact crater and/or environmental shifts that adversely affected the food plants utilised by broad-crowned sauropods (and stegosaurs). This is further supported by the expectation of a reduction in the scale of any mass extinction by the backward smearing of origination times in the PDE (Wagner 2000b). The remaining time periods of the Late Triassic–Jurassic seem to be largely controlled by sampling biases (Upchurch and Barrett 2005), although the Norian may at least represent a small peak in diversity.

The Cretaceous record is more difficult to interpret as many of the sampling biases suggest contrasting fluctuations in diversity. The Berriasian–Barremian does appear to be an interval of genuinely low diversity. However, increased ‘gappiness’, at least in the very earliest part of the Early Cretaceous (i.e. the Berriasian), may be a result of a lack of preservation of the environment, rather than true fluctuations in diversity. Nevertheless, this cannot account for the remainder of the earliest Cretaceous,

indicating that this represented a truly depauperate time interval. This contrasts with previous studies that have proposed a diversity peak in the Valanginian–Barremian (Hunt *et al*. 1994; Barrett and Willis 2001; Lloyd *et al*. 2008). The Aptian–Albian may represent a genuine peak in diversity; however, at least some of this appears to be influenced by sampling biases (Upchurch and Barrett 2005), suggesting it may only be a small peak. Diversity in the Cenomanian–Santonian is difficult to elucidate, with rarefaction suggesting moderately high diversity while residuals indicate relatively low diversity. However, this time period has been overlooked in comparison to many other Mesozoic intervals, with few diagnostic remains known until relatively recently, and poor exposures in many parts of the world (i.e. Europe and North America); thus, it is possible that this remains under-sampled.

PDE shows an incremental increase in diversity from the early Campanian–late Campanian. This is followed by a slight decline in the early Maastrichtian, before diversity plummets in the late Maastrichtian. However, this drop in the PDE is likely to be a result of the Signor-Lipps effect. Residuals, on the other hand, suggest low diversity in the early Campanian, but then produce contradictory signals for the late Campanian–early Maastrichtian. Rarefaction does not recover higher diversity levels than the rest of the mid-Late Cretaceous and finds no evidence for a Campanian–Maastrichtian decline. It seems likely that at least some of these latest Cretaceous diversity levels are the product of sampling biases (Upchurch and Barrett 2005).

Although the western European rock record is not a useful proxy for global sauropodomorph diversity, it is closely correlated with the diversity of taxa from this region. This suggests that a global compilation of rock outcrop area may provide a strong correlation with global diversity (Haubold 1990; Wall *et al*. 2009); however, testing of this hypothesis is not possible at the moment because stage level global rock outcrop metrics are currently unavailable. It would be useful for future studies to also

consider similar comparisons for other regions (see Mannion, in press [a]), given that no single region may provide a sufficiently accurate proxy for global diversity.

There is evidence to suggest that sea level exerts a biotic influence on sauropodomorph diversity. Both a Kimmeridgian peak and putative late Maastrichtian decline correspond to a peak and lowering of sea level, respectively. Terrestrial regions may have become isolated in the Kimmeridgian as a consequence of high sea level, resulting in allopatric speciation, while a late Maastrichtian regression may have led to extinction events as a consequence of the biotic mixing of previously isolated areas (Bakker 1977; Horner 1983; Weishampel and Horner 1987; Upchurch and Barrett 2005). Several time intervals represent negative correlations between diversity and sea level: these may also reflect biotic events, in that marine transgressions decrease habitat size and can lead to extinction (Dodson 1990; Upchurch and Barrett 2005), although abiotic factors such as a reduction in the terrestrial rock record may have also contributed (Markwick 1998). The overall lack of correlation in the Late Cretaceous supports the above result that titanosaurs (which constituted nearly all Late Cretaceous sauropods) showed a preference for inland terrestrial environments, and thus sea level should have a limited or indirect effect on their diversity.

This study illustrates that comparison and use of multiple proxies and methods is imperative in any attempt to discriminate genuine diversity from the biases of our uneven sampling of the rock record. Furthermore, these analyses highlight the importance of looking at particular taxonomic groups (i.e. sauropodomorphs) in conjunction with more inclusive clades (i.e. dinosaurs). Although analysing a single group of animals in isolation may have limitations in terms of elucidating general macroevolutionary patterns (i.e. the results may only show what that particular group is doing), at a broader scale fluctuations in one group can be dampened by signals in others. For sauropodomorphs, this seems to be particularly problematic, as previous studies have noted that their diversity does not strongly correlate with that of

ornithischians and theropods (Weishampel and Jianu 2000; Upchurch and Barrett 2005; Barrett *et al*. 2009). However, more rigorous testing of the effects of sampling for these two groups is also required.

3. The completeness of sauropodomorph specimens has fluctuated throughout geological time, with peaks in the Hettangian, Late Jurassic and Late Cretaceous, and troughs in the Rhaetian, early Middle Jurassic, earliest Cretaceous and early Late Cretaceous. Fluctuations in the Jurassic and Early Cretaceous correlate negatively with sea level, suggesting that high sea levels diminish the preservation potential of terrestrial organisms by decreasing the availability of land area (Markwick 1998). The application of completeness metrics to sauropodomorphs also reveals the surprising result that the fossil record for Cretaceous forms is poorer than that for Triassic and Jurassic ones. This may reflect the preference for inland habitats displayed by the Cretaceous titanosaurs.

The results of Benton (2008a, b) for all dinosaurs, and the current analyses for sauropodomorphs, agree that type specimen completeness has increased since 1830. However, this 'trend' masks a more complex picture in which completeness scores fluctuate from decade to decade, and from year to year, and in which there is no discernible trend from 1900, 1940, 1970 or 1990 to the present. It seems that the type specimens described during the earliest phase of dinosaur palaeontology (1830-1900) were, on average, less complete than those described since 1900. However, this does not reflect an 'improvement' in taxonomic practice: rather, it seems inevitable that the specimens discovered early in a field's history will be genuinely 'new', irrespective of their completeness, and will receive a name. As the number of type specimens and completeness of specimens available for comparison increases through time, many of the early type specimens will be shown to be invalid because their once diagnostic characters have become historically 'obsolescent' (Wilson and Upchurch 2003). The fact that average type specimen quality has not increased since 1900, and indeed is

particularly low for the current decade, suggests that palaeontologists have continued to name new taxa on the basis of very incomplete specimens. This interpretation is likely to hold true for all dinosaurs, not just sauropodomorphs, because re-analysis of Benton's data also indicates that there is no trend towards increasing type specimen completeness through more recent historical time. However, future studies should test this proposal by examining theropods, ornithischians and sauropodomorphs separately.

In general it seems that SCM1-2 and CCM1-2 produce the same overall patterns through geological and historical time, but this is a single case study of sauropodomorphs and it is possible that these metrics might diverge from each other when applied to other organisms.

4. The palaeolatitudinal distribution of sauropodomorphs and ornithischians has varied through time; however, more noteworthy, is that these two clades seemed to develop a distributional skew, particularly during the Cretaceous, becoming more marked in the Late Cretaceous. This distribution seems to be largely controlled by collecting effort, but 'removal' of sampling still results in a distributional skew, suggesting that the two clades did undergo some sort of palaeolatitudinal separation during the Cretaceous (Barrett and Butler 2008). It is possible that this skew relates to environmental preferences. While titanosaurs seemed to prefer inland environments, the dominant Late Cretaceous ornithischians (hadrosaurids) showed a preference for coastal settings (Barrett and Butler 2008). Thus, it is possible that these environmental preferences drove sauropods and ornithischians to inhabit different niches and therefore different palaeolatitudes. This niche partitioning may relate to dietary preferences, i.e. the distributions of particular plant groups, although previous studies have found little evidence for such correlations (Barrett and Willis 2001; Butler et al. 2009a, b). Additionally, sauropodomorph diversity is high in tropical ('summerwet') and humid climes, whereas ornithischians (although present in such regions) are largely restricted to warm ('winterwet') and cold temperate zones. A preference for different climatic zones,

perhaps interlinked to floral distributions and the different dietary needs of the two groups, may be an additional cause for their palaeolatitudinal habitat separation.

5. Sauropod and ornithischian tracksite abundance show similar fluctuations to one another through the Jurassic and Early Cretaceous; however, the two display very different variations in abundance in the Late Cretaceous, indicating a degree of disparity between these two herbivorous clades, which may be related to the palaeolatitude patterns outlined above.

Sauropod tracksite abundance and taxic diversity are also correlated, which probably reflects sampling: i.e. well-sampled time periods preserve high generic counts but also large numbers of individuals.

Fluctuations in the rock record appear to exert a small, but notable, influence on changes in tracksite abundance through time. There is evidence that abundance in the Jurassic and Early Cretaceous is controlled to some extent by taphonomic and sampling biases; however, the Late Cretaceous seems to be largely removed from these effects, although this may reflect issues pertaining to under-sampling as outlined above. Sea level also appears to affect abundance during the Jurassic and may reflect the positive association between non-titanosaurs and coastal environments. Similarly, the lack of correlation between sea level and tracksite abundance in the Cretaceous might be a consequence of the inland preference displayed by titanosaurs (which comprise the majority of Cretaceous sauropods).

6. The disarticulation sequence of sauropodomorphs begins with the loss of extremities, followed by a gradual loss of elements from the front, back and lower parts of the body. Complete skeletons of basal sauropodomorphs are more commonly preserved than derived sauropods: this may relate to body size as derived forms tend to be much larger animals. Although large animals may be more likely to be preserved (Behrensmeyer *et*

al. 1979), the large amount of sediment needed for their burial makes complete preservation extremely. This may explain why so many basal forms are known from relatively complete skeletons while many derived sauropods are often known only from isolated bones.

Future work

1. Although the results from the environmental analyses indicate that wide-gauge trackways are produced by titanosaurs, Henderson's (2006) hypothesis that they are produced by sauropods above 12 tonnes deserves attention. This could be tested by partitioning the current body fossil dataset along body size rather than taxonomy (i.e. below and above 12 tonnes replacing non-titanosaurs and titanosaurs, respectively) and then testing for environmental associations as before. Additionally, other sauropodomorph divisions could be examined (e.g. non-sauropods and sauropods) as well as testing for environmental associations in other dinosaur (or non-dinosaur) groups (e.g. Middle Jurassic theropod clades).

An additional limitation to these results relates to the choice of environmental partitioning. A simple partition of inland and coastal is admittedly crude and it is possible that finer-scale analyses may produce results that differ, perhaps demonstrating that it is in fact a subset of inland environments that titanosaurs display a preference for, e.g. arid environments. Future work needs to investigate palaeoecology using actual depositional environments (i.e. fluvial, aeolian, etc.), rather than just geographical position (i.e. inland and coastal), which lump quite different environments. However, currently, the means to implement such analyses are not available because of a lack of information in the literature on depositional environments.

Although chi-square tests are an appropriate method for investigating environmental associations, other statistical tests may enable a more refined study. For example, multifactorial analyses, such as Akaike's Information Criterion, could be used to more precisely determine which environments were most closely associated with each group (Jablonski 2008; Friedman 2009).

2. This study represents the most thorough investigation into sauropodomorph diversity to date; similar methods could be applied to ornithischian and theropod diversity. Although the results from the current study indicate that the Jurassic/Cretaceous boundary represents a genuine extinction event, the collection of rock outcrop area data (using similar methods of collection as Smith and McGowan 2007) would allow this to be investigated in a more rigorous fashion. Additionally, use of new online resources, such as the *OneGeology* project (www.onegeology.org), may allow a global compilation of rock outcrop area and enable the testing of the effects of global rock outcrop on global diversity. The methods utilised here could also be applied to the investigation of other groups with extensive ghost ranges (e.g. lissamphibians) and to key events such as extinctions (e.g. the K/P event) or radiations (e.g. the Cambrian 'explosion').

One key limitation of these analyses is the poor dating of many outcrops across the globe and throughout the Mesozoic. This adds much ambiguity to diversity curves and may obfuscate peaks and troughs. Increased stratigraphic work is improving this to some extent, but many regions of the world (e.g. the Cretaceous of China) still have large-scale problems. One possible way to attempt to ameliorate this problem in future analyses would be to implement sensitivity approaches, whereby the effects of uncertainties in the ages of rocks (and thus species) are examined by varying the ages between different values. This could be repeated numerous times, with an overall randomised diversity curve produced.

Although this work has made some attempt to correct for long-term trends by time-slicing, future analyses should also statistically test for the effects of trend, temporal autocorrelation and seasonality on raw data series. These problems could be ameliorated through use of statistical procedures such as detrending, first and generalised differences, and generalised least squares (McKinney 1990; Alroy 2000; Smith and McGowan 2007; Marx and Uhen 2010).

3. The completeness of other dinosaur (and other vertebrate) groups could be investigated: this would allow thorough testing of Benton's claims for increasing completeness through historical time but, perhaps more significantly, would contribute to creating sampling metrics for future diversity studies. Additionally, more rigorous evaluation of the correlation between a completeness metric and observed diversity is required, as well as comparisons between completeness metric scores and other measurements used as fossil record sampling proxies (e.g. numbers of fossil-bearing formations, sedimentary rock outcrop area) and with factors that might control preservation rates (e.g. sea level, relative extent of different facies types, erosion rates etc.). Investigations into the potential effect of body size on completeness may also represent interesting avenues for future research, as well as the related effects of taphonomy.

4. This work has produced the first rigorous study of the palaeolatitudinal patterns of dinosaurs. This could be expanded to include all dinosaurs, using data from *The Paleobiology Database*. Similarly, along with using residuals, rarefaction methods could also be used for testing for the effects of sampling biases. Investigations into the effects of the amount of terrestrial land present in each palaeolatitudinal bin could also prove useful in an attempt to 'remove' sampling biases. Temporal abundance patterns of body fossils could also be analysed. The study of latitudinal patterns has so far been restricted to neontological and palaeo-invertebrate analyses: as well as investigating patterns in dinosaurs, other palaeo-vertebrate groups could also be examined.

Numerous factors exert an influence on the modern day latitudinal biodiversity gradient (LBG; Willig *et al*. 2003), although climate has been suggested to be the dominant driver (Hawkins *et al*. 2003; Turner 2004; Field *et al*. 2009). For example, during warmer periods there is a tendency for poleward and/or elevational shifts of organisms, with the magnitude of future effects expected to increase with latitude (Parmeson and Yohe 2003; Root *et al*. 2003; Colwell *et al*. 2008), although the greatest extinction risk to

ectotherms is in the tropics (Deutsch *et al*. 2008; Huey *et al*. 2009). A long-term negative correlation between temperature and biodiversity has also been noted in the fossil record (Mayhew *et al*. 2008). Consequently, this topic is of great interest in projecting biodiversity loss driven by present day climate change and exploring why certain regions have higher biodiversity than others. Examination of this topic in the past, using dinosaurs, may enable a better understanding of how modern day faunas might respond to environmental perturbations.

5. Tied in with the environmental analyses, future tracksite work should investigate potential preservational biases. Analyses should be implemented to examine how different substrates affect preservation and whether body size/mass impacts on the likelihood of a certain track type being preserved in a particular type of environment. Additionally, a review of the narrow/wide-gauge dichotomy needs to be implemented, with more clarification as to whether these merely mark two end members of a spectrum and if non-titanosaurs can 'create' wide-gauge trackways.

6. With regards to taphonomic and disarticulation patterns, the effect of different depositional environments on preservational potential needs further investigation. Although the current study examined inland vs. coastal, these are crude divisions (see above) that group together a number of disparate environments. Future studies should attempt to look at this problem on a finer scale; however, problems remain due to a lack of detailed environmental data for the majority of specimens, although an increasing number of studies are recognising the importance of understanding the taphonomic history of newly discovered specimens (e.g. González Riga and Astini 2007). Hopefully, other new discoveries will receive similar treatments, providing a new and improved dataset of depositional environments.

7. Lastly, as our understanding of Sauropodomorpha increases (particularly with regard to the taxonomic content and intra-relationships of Titanosauria), many of these analyses could be re-run with updated datasets.

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APPENDIX

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